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A SYSTEMATIC STUDY OF THE SALICACEÆ.

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IN attempting a discussion of the Salicaceæ from the standpoint of their ancestry, as presented in the woody structure of the mature stem, a first step involves comparison with previously existing forms and with closely related types now extant, in order to determine the general phylogenetic sequence and the position which the group at present occupies. We are therefore led, at the very outset, to ask: (1) what is the nature of the evidence to be derived from paleontology, and what is the bearing of such evidence; and (2) what is the nature and bearing of the evidence to be derived from the structure of existing species? The Salicaceæ as we now know them, are altogether confined to two genera — Populus and Salix — of very wide distribution in north temperate latitudes whence they extend beyond the extreme northern limit of tree growth within the polar circle, being there reduced to prostrate shrubs. It is quite possible that the family may have been more extensive in early or middle Mesozoic time, but the evidence now available as derived from their fossil remains, leads us to the supposition that it has not been, at any previous time in its history, of a more comprehensive character. In common with many other

families of Dicotyledons, it made its appearance very abruptly in the Cretaceous age, whence it has continued through succeeding formations, appearing with prominence in the Pleistocene where its remains form a distinctly connecting link with existing species, with many of which they are more or less identical.

An analysis of the Salicaceæ based upon the enumeration of the Index Kewensis, shows that there are at the present time no less than two hundred and seventy recognized species, an altogether unusual proportion for a family embracing such a limited number of genera. Of these, twenty-two belong to the genus Populus, while two hundred and forty-eight belong to the genus Salix.

The poplars are preëminently a type peculiar to the northern hemisphere, and in their chief aspects they have a strong tendency to a boreal habit, the one exception to be met with in the subtropical *P. mexicana* offering no material contradiction of this law. *P. ciliata* of the Himalayas, though reaching a latitude far below that of most representatives of the genus, nevertheless conforms to the temperate habit of the group by virtue of the somewhat high elevations at which it grows. Six species range from Japan through China, Mongolia, and Siberia to Central Asia, while the western extension of the genus is carried through northern and central Europe as far south as Spain and Italy. In the western hemisphere, no less than ten species are to be met with, ranging from Mexico as the extreme southern extension, thence northward as far as the arctic circle where *P. balsamifera* appears to establish the limit of development. The very remarkable isolation and localization of the various species is one of the most prominent features disclosed by an examination of these plants. *P. mexicana* is confined to Mexico and similarly *P. ciliata* is peculiar to the Himalayas. *P. adenopoda* is restricted to China as *P. sieboldii* is to Japan; while *P. przewalskii* of Mongolia and *P. pruinosa* of Siberia, as also *P. euphratica* of Central Asia, give emphasis to this strong segregation, since they are as wholly distinct from the European and American species as are those of the last two regions from one another. In only one instance does there seem to be any

connecting form. This is presented in the ubiquitous balsam poplar of Asia and North America which not only serves to connect the types of both hemispheres, but it gives to the genus a greater range of latitude than any other species. Evidence of this nature would naturally lead to the supposition that *P. balsamifera* may represent a more generalized type ancestral to many of the associated species. But on the other hand, the very extensive distribution of distinct species occupying essentially isolated and often very widely separated regions, suggests a more general dispersal during Cretaceous and Tertiary time, and their eventual restriction to more limited areas through the operation of important physical agencies, with the survival of the more resistent but not necessarily the oldest species. In particular it is conceivable that such restriction may have been brought about in one of two ways: (1) the elimination of the ancestral type or types, of which *P. balsamifera* may possibly be regarded as the sole survivor, would tend to leave the descendants isolated as now found; (2) the ancestral forms having disappeared at a comparatively early period in the history of the genus, more recent physical changes in the earth's crust and in climatic conditions would give rise to more or less profound alterations in distribution in such a way as to effect a more pronounced segregation and localization. That such causes have been operative in glacial times is well known, and they have left a very definite impress upon the distribution of the existing flora of this continent, as particularly indicated by the various forms of alpine vegetation (Gray, '89, vol. 1, p. 122; vol. 2, pp. 24, 142, 260) and by such special arborescent forms as *Larix americana*, Sequoia, *Pseudotsuga douglasii*, etc. (Penhallow, : 04).

From this analysis it appears that there are twelve species of poplar peculiar to the Old World and nine species peculiar to the New World, with one species common to both. From this circumstance it would be natural to conclude that this is essentially an Old World genus, but the slight numerical difference noted would make such a generalization unsafe without confirmatory evidence derived from the paleontological record to which appeal must also be made for an answer to several other questions that have already arisen.

Like the poplars, the willows are a type essentially peculiar to the temperate regions of the northern hemisphere, though they represent adaptation to a greater diversity of climatic conditions and thereby greatly extend the northern and southern range of the family as a whole. With the exception of about 2 percent —an altogether insignificant proportion—they are of a continental character. Nevertheless, in the *S. junghuhniana* of Java, *S. sumatrana* of Sumatra, *S. canariensis* of the Canary Islands, *S. madagascariensis* of Madagascar, and *S. occidentalis* of the West Indies, types which are strongly segregated and localized, their very restricted range is in close proximity to the corresponding vegetation of the continental areas in which they must have had their origin and from which they must have been isolated at a comparatively late period as shown by Wallace ('80). It is these insular forms which are chiefly concerned in the extreme southern extension of the genus, since the six Mexican and eight north African species range considerably farther north. The extreme isolation of *S. humboldtiana* in South America affords at once an illustration of the extent to which dispersal must have been carried in former geological times, and of the potency of the influences which have tended to a greater restriction of geographical area.

Of the one hundred species common to Asia, twenty-four are found within the Himalayan region, while seventy-three are more peculiar to the temperate and boreal regions of Japan, China, Siberia, and Central Asia. In Europe no less than eighty-four species give a range to the genus which extends from the Mediterranean on the south to the polar regions where the very diminutive *S. polaris* with an extreme height of about 3.3 cm., defines the northern limit of growth. In North America, apart from Mexico, seventy-two species similarly extend the genus over a wide range of latitude, their northern limits being defined by the boreal *S. ovalifolia* which also ranges southward on the summits of lofty mountains, as far as Mount Washington in New Hampshire. Ubiquitous species are much more common than among the poplars, and there are no less than 23 which are more or less common to the several continental regions as exhibited by the following synopsis.

Community of Species of Salix.

Europe and Asia	14
Europe and North America	7
Europe and Africa and Asia	1
Asia and Africa	1
	23

In determining these relations, the very pronounced isolation of the Japanese and Himalayan species stands out with great prominence and lends emphasis to the idea of segregation in a previously continuous flora. From the facts thus presented, it is obvious that the willows are preëminently an Old World genus, and that, although their dispersion has a tendency to greater diffuseness than in the case of the poplars, like them they essentially belong to temperate regions, and their tendency is on the whole boreal, rather than austral; so that with respect to the Salicaceæ as a whole, it may be said to be a distinctly temperate and boreal family of wide dispersion within the northern hemisphere, with its center of distribution in Asia where it presumably had its origin. A summary of these geographical relations will serve to make the foregoing analysis more clear.

In the light of these facts it becomes pertinent to ask whether the family as now known represents a type of vegetation which is yet in process of evolution, if it is a side line which has recently attained to the full limit of development and which is therefore terminal, or if it attained the culmination of its development in some previous geological age and is now in a state of decline comparable with that exhibited by the Lycopodiaceæ and the Equisetaceæ. The comparatively recent origin of these plants, if we are to judge them by the standards which have been set by other groups, the general phylogeny of which is fairly well known, would naturally lead us to support the first hypothesis or at least the second, and to reject the third as improbable. But such generalizations are unsafe unless supported by other well established data, and it therefore becomes necessary to inquire somewhat particularly into the nature of the evidence afforded by the geological history of these plants.

Geographical Distribution of the Salicaceæ.

	Old World.									New World.			
	Malaya.	Java.	Sumatra	India. Himalayan Region.	Other parts of Asia.	Madagascar.	Canary Islands.	Africa.	Europe.	South America.	West Indies.	Mexico.	North America.
Salix	1	1	1	24	73	1	1	8	84	1	1	6	72
	100					10			84	80			
248	194									80			
Percent	0.4	0.4	0.4	9.68	29.43	0.4	0.4	3 22	33.87	0.4	0 4	2.41	29.03
	40.32%					4.03%			33.87%	32.26%			
	Duplications 78.22% Total 70.03%									Duplications 32.26% Total 29.97%			
Populus				1	6				6			1	9
22	13									10			
Percent				4.54	27.27				27.27			4.54	40.91
	Duplications 50.00% Total 56.41%									Duplications 45.45% Total 43.59%			
Salicaceæ 270	Duplications 78.88% Total 69.25%									Duplications 33.33% Total 30.75%			

Our knowledge of the fossil Salicaceæ had its origin in the work of Heer upon the fossil plants from the Cretaceous formation of Greenland, through his description of *Populus primæva*. The occurrence of this species in the Kome beds not only afforded the first real evidence of the occurrence of these plants in previous geological time, but it at once served to suggest the essentially primitive character of the Salicaceæ as a whole among Dicotyledons—an idea subsequently strengthened by the discovery of both Salix and Populus in the Potomac formation, as well as in the Kootanie beds of Montana. This idea, then, has persisted to the present day and finds repeated expression in the various treatises on fossil plants, although the acceptance of such a view is not based in any case, upon trustworthy facts derived from a critical comparison of distribution, a knowledge of the phylogeny of the group, or an acquaintance with the anatomy of either recent or extinct species. Paleontologically it is of interest to determine the position of the Salicaceæ relatively to the other families associated with it in the Cretaceous and Tertiary deposits, and for this purpose the flora carefully compiled by Dr. Knowlton ('98) offers the most reliable basis now available. Among forty-five families of angiosperms now known to constitute the flora of the Cretaceous and Tertiary ages in North America, it will be found that, geologically speaking, the Salicaceæ is by no means the primitive group which seems to be implied by the position usually assigned to it, but that it really occupies a position which is the twenty-fourth in a series based upon the percentage ratio of occurrence in the two great geological periods. Such a series has as its lowest member, the Proteaceæ which is preëminently a Cretaceous family, bearing to the Tertiary the ratio of 19 : 0. The same is also true of the Menispermaceæ with a ratio of 17 : 0, closely followed by the Araliaceæ (6 : 0) and the Euphorbiaceæ (2 : 0). At the other extremity of the series we find such families as the Hydrocharidaceæ (0 : 2), Lemnaceæ and Simarubaceæ (0 : 3), Typhaceæ (0 : 4), Onagraceæ (0 : 5), Naiadaceæ (0 : 7), Zingiberaceæ (0 : 17), and the Cyperaceæ (0 : 20), all of which are manifestly typical Tertiary plants. About midway of the series the Salicaceæ are associated with the Urticaceæ with a ratio of 1 : 1.47 and with the somewhat similarly distributed Platanaceæ,

Myricaceæ, Cornaceæ, and Sapindaceæ. There is thus a very strong suggestion (1) that the Salicaceæ is in no sense a primitive family from the standpoint of geological succession, and (2) it is, as a whole, much more characteristic of the Tertiary than of the Cretaceous, more especially as a closer analysis of the one hundred and forty-one known species shows that this rule applies to each of the constituent genera as well as to the entire family, though more conspicuously to the genus Populus than to Salix. Thus we find that the forty-seven Cretaceous species embrace 34 of Populus and 23 of Salix, while the eighty-four Tertiary species embrace 59 of Populus and 25 of Salix, making the ratio of Cretaceous to Tertiary 1 : 1.75 for the former and 1 : 1.09 for the latter — ratios which tend to indicate that these two genera and so the family as a whole, were in process of development even in Tertiary time, a conclusion which is in apparent accord with the recent origin of the family.

Comparison of Cretaceous and Tertiary Floras.

	Seq. No.	Ratio.	Cretaceous No.	Cretaceous Percent.	Tertiary No.	Tertiary Percent.
Proteaceæ	1	19 : 0.00	19	1.09	0.00	0.00
Menispermaceæ	2	17 : 0.00	17	0.98	0.00	0.00
Araliaceæ	3	6 : 0.00	6	0.34	0.00	0.00
Euphorbiaceæ	4	2 : 0.00	2	0.11	0.00	0.00
Passifloraceæ	5	1 : 0.00	1	0.06	0.00	0.00
Asclepiadaceæ	5	1 : 0.00	1	0.06	0.00	0.00
Myoporineæ	5	1 : 0.00	1	0.06	0.00	0.00
Convolvulaceæ	5	1 : 0.00	1	0.06	0.00	0.00
Bromeliaceæ	5	1 : 0.00	1	0.06	0.00	0.00
Casuarineæ	5	1 : 0.00	1	0.06	0.00	0.00
Sterculiaceæ	6	1 : 0.13	15	0.86	2	0.11
Myrsineæ	7	1 : 0.17	6	0.34	1	0.06
Myrtaceæ	8	1 : 0.18	11	0.63	2	0.11
Hamamelaceæ	9	1 : 0.25	4	0.22	1	0.06
Magnoliaceæ	10	1 : 0.31	45	2.60	20	1.15
Thymeleaceæ	11	1 : 0.33	3	0.17	1	0.06
Anonaceæ	11	1 : 0.33	3	0.17	1	0.06
Araliaceæ	12	1 : 0.36	47	2.71	17	0.98
Sapotaceæ	13	1 : 0.50	4	0.22	2	0.11
Lauraceæ	14	1 : 0.56	69	3.98	39	2.25
Vitaceæ	15	1 : 0.61	26	1.50	16	0.92

	Seq. No.	Ratio.	Cretaceous No.	Cretaceous Percent.	Tertiary No.	Tertiary Percent.
Celastraceæ	16	1 : 0.70	30	1.73	21	1.21
Leguminosæ	17	1 : 0.72	32	1.84	23	1.32
Araceæ	18	1 : 0.75	4	0.22	3	0.17
Ebenaceæ	19	1 : 0.76	13	0.75	10	0.57
Ericaceæ	20	1 : 0.94	18	1.03	17	0.98
Bignoniaceæ	21	1 : 1.00	1	0.06	1	0.06
Apocynaceæ	21	1 : 1.00	1	0.06	1	0.06
Alismaceæ	21	1 : 1.00	2	0.11	2	0.11
Platanaceæ	22	1 : 1.26	15	0.86	19	1.09
Myricaceæ	23	1 : 1.29	24	1.38	31	1.79
Urticaceæ	24	1 : 1.47	65	3.70	96	5.54
Salicaceæ	24	1 : 1.47	57	3.29	84	4.79
Cornaceæ	25	1 : 1.50	12	0.69	18	1.03
Sapindaceæ	26	1 : 1.62	24	1.38	39	2.31
Cupuliferæ	27	1 : 1.71	94	5.43	161	9.30
Caprifoliaceæ	28	1 : 1.82	17	0.98	31	1.79
Rhamnaceæ	29	1 : 1.96	26	1.50	51	2.94
Aquifoliaceæ	30	1 : 2.00	9	0.51	18	1.03
Aristolochiaceæ	30	1 : 2.00	2	0.11	4	0.22
Tiliaceæ	30	1 : 2.00	1	0.06	2	0.11
Rosaceæ	31	1 : 2.89	9	0.51	26	1.50
Juglandaceæ	32	1 : 3.00	13	0.75	39	2.25
Liliaceæ	32	1 : 3.00	2	0.11	6	0.34
Altingiaceæ	33	1 : 4.00	1	0.06	4	0.22
Nymphæaceæ	34	1 : 6.00	2	0.11	12	0.69
Gramineæ	35	1 : 6.50	2	0.11	13	0.75
Anacardiaceæ	36	1 : 7.50	4	0.22	30	1.73
Palmaceæ	37	1 : 18.0	1	0.06	18	1.03
Musaceæ	38	0 : 1.00	0	0.00	1	0.06
Eriocaulonaceæ	38	0 : 1.00	0	0.00	1	0.06
Elæagnaceæ	38	0 : 1.00	0	0.00	1	0.06
Droseraceæ	38	0 : 1.00	0	0.00	1	0.06
Rutaceæ	38	0 : 1.00	0	0.00	1	0.06
Polygonaceæ	38	0 : 1.00	0	0.00	1	0.06
Rubiaceæ	38	0 : 1.00	0	0.00	1	0.06
Berberidaceæ	38	0 : 1.00	0	0.00	1	0.06
Piperaceæ	38	0 : 1.00	0	0.00	1	0.06
Hydrocharidaceæ	39	0 : 2.00	0	0.00	2	0.11
Lemnaceæ	40	0 : 3.00	0	0.00	3	0.18
Simarubaceæ	40	0 : 3.00	0	0.00	3	0.18
Typhaceæ	41	0 : 4.00	0	0.00	4	0.22
Onagraceæ	42	0 : 5.00	0	0.00	5	0.28
Naiadaceæ	43	0 : 7.00	0	0.00	7	0.45
Zingiberaceæ	44	0 : 17.0	0	0.00	17	0.98
Cyperaceæ	45	0 : 21.0	0	0.00	21	1.21

The succession exhibited in this table brings into prominence the idea that such families as the Leguminosæ, Vitaceæ, Ericaceæ, Magnoliaceæ, Convolvulaceæ, etc., are inferior to the Salicaceæ which is, in turn greatly inferior to the Cyperaceæ from an evolutionary point of view when considered solely in the light of their geological succession; but the sequence which is thus established is found to be utterly at variance with that usually adopted on the basis of morphological evidence which for obvious reasons must be regarded as the more trustworthy guide. Such discrepancies between the morphological and the geological succession, in our opinion, should not be so great as seem to be suggested by the available data, and no doubt they will diminish as our knowledge of the fossil representatives becomes more nearly complete, but that such discrepancies may be anticipated, and that they are to some extent to be regarded as a normal result of rapid evolution along many diverse lines of development, is a reasonable supposition. The Mesozoic age was a period of very great diversification among plants in consequence of the profound physical changes which had taken place in the atmosphere as well as in the configuration of the surface of the earth, and the fact that as a product of previous development, plants were in a condition to be widely and profoundly influenced by comparatively slight modifications of external conditions. The very great number of families and genera and even species of angiosperms which abruptly appeared in the Cretaceous, presenting as they did types of vegetation wholly unlike those of previous geological periods, indicates that the parental forms must have had their origin in the early Mesozoic and possibly as far back as the Permian, since our acceptance of the general principles involved in De Vries' mutation theory does not permit us to consider as possible, such phenomenal transitions as would be involved in the application of that theory to the case under consideration; while on the other hand all paleontological evidence, as well as the evidence derived from existing types, confirms us in the belief that such highly organized forms could have arisen in the main, only through a long series of transitional forms occupying great periods of time. For the same reasons also, we are led to believe that the great

diversification of the Cretaceous flora must have been initiated at correspondingly early periods, though the general succession of types of which we have knowledge, would indicate that it did not gain full expression until about the time of the Middle Cretaceous. This diversification was no doubt the natural response of vegetation to the profoundly changed physical conditions, chiefly climatic, which followed the close of the Carboniferous age and resulted in a diminution of the carbon dioxide of the atmosphere to about one-twentieth of its original volume with a consequent reduction of atmospheric density; a general purification of the atmosphere whereby it became more readily penetrated by the sun's rays; a lower and less equable temperature with more localized climates, and conditions which, as a whole, were more favorable to a more varied mesophytic type of vegetation. Under such circumstances, involving as they did a more abundant supply of oxygen, the general activities of growth became greater; the transformation of carbon dioxide into assimilable products became proportionately larger; in response to the more favorable conditions of light and air, the foliage became broader and acquired an increased functional capacity; and with the augmentation of capacity for the storage of energy thus made possible, there were increased possibilities of, as well as strong tendencies toward diverse development in which special mutations no doubt played an important part, in response to even comparatively slight variations in environmental conditions. From this point of view it is not difficult to understand that among the numerous offshoots from the main line of descent there would be very varying degrees of activity, and it is readily conceivable that plants of a low phylogenetic position might be held in numerical abeyance for a long time, while others, originating at a higher level but more favorably situated and more capable of responding to their environment, might at once outdistance them in number of species or of varietal forms. Under such circumstances the geological succession might lead to erroneous conclusions as to the true phylogenetic sequence. Such a view is suggested and supported by a comparison of many well known examples among existing species. In this way it would be possible for a relatively superior type of organ-

ization, and one occupying a higher position in the morphological scale, to occupy an inferior position in the geological scale, and thus to appear antecedent to morphologically inferior types.

From the foregoing considerations it is clear that geological data cannot be wholly relied upon to furnish a correct solution of questions bearing upon the evolution of plant forms, and this is especially true with respect to the broad-leaved angiosperms for reasons which will be described more fully on a subsequent page. Interesting as these various speculations may be, as applied to the Salicaceæ they nevertheless lack an essential foundation which can be obtained only by a more searching scrutiny of the family as a whole, and of its component genera, with respect to their more detailed distribution in Cretaceous and Tertiary time, as well as at present.

Nowhere has it been possible to obtain so complete a record of the Cretaceous flora as from the exposures to be met with in Greenland and the United States, and the systematic way in which the various horizons have been worked out, affords a very satisfactory basis for a knowledge of the geological succession of species and genera. In his studies of the Cretaceous flora of Greenland, Heer found that out of a total of 88 species from the Kome beds, only 5.68 % were Monocotyledons, while the Dicotyledons were represented solely by *Populus primæva* to the extent of 1.14 %. In the Cenomanian flora of the Atane beds, there was a remarkable increase of Dicotyledons amounting to 50.09 % in a total of 177 species; while from the Patoot beds of the Senonian, 59.48 % were Dicotyledons out of a total of 116 species, thus showing a marked development of this type of plants toward the close of the Cretaceous. This ratio between the three divisions of the flora also appears to extend very largely to the Salicaceæ in particular, with respect to which we find 27.40 %, 42.40 %, and 30.10 % respectively for the three horizons. An analysis of the family, however, shows that this relation does not altogether hold in detail for the individual genera. Thus in Salix the percentages are 41.40, 41.40, and 17.20 which approximates to the results for the family as a whole with respect to the very evident falling off in the Upper Cretaceous. Nevertheless this is much more marked in the

genus than in the family, and suggests that the former is in process of decline, a conclusion which seems to be directly opposed by the evidence afforded by the ratio of extinct and living forms. Populus gives 18.10%, 43.10%, and 38.60% for the three horizons with a maximum development in the Middle Cretaceous.

Distribution of Salicaceæ in Cretaceous of United States.

SALIX.

	Lower.	Middle.	Upper.
Salix stantoni			×
mattawanensis		×	
meekii		×	
protæfolia	×	×	
" *flexuosa*	×	×	
" *lanceolata*		×	
" *linearifolia*		×	
" *longifolia*		×	
cuneata		×	
deleta		×	
hayei		×	
inequalis	×		
membranacea	×		
nervillosa		×	
newberryana	×		
pacifica			×
purpuroides	×		
sp.	×		
sp.			×
sp.	×		
sp.			×
sp.		×	
sp.			×
Saliciphyllum ellipticum	×		
longifolium	×		
parvifolium	×		
Species 26	11	12	5
Percentage distribution	42.3%	46.1%	19.2%

Distribution of Salicaceæ in Cretaceous of United States.

POPULUS.

	Lower.	Middle.	Upper.
Populus berggreni	×	×	
hyperborea		×	
stygia		×	
mutabilis	×		
lævigata			×
arctica			×
problematica			×
obovata			×
melanarioides			×
wardii			×
mutabilis ovalis?			×
apiculata	×	×	
aristolochioides		×	
auriculata	×		
cordifolia		×	
elliptica		×	
harkeriana		×	
latidentata			×
kansaseana		×	
longior			×
leuce		×	
microphylla		×	
potomacensis	×		
protozadachi			×
rectinervata			×
rhomboidea			×
trinervis			×
sp.			×
sp.			×
sp.			×
Populites tenuifolius		×	
cyclophylla		×	
elegans		×	
lancastriensis		×	
litigiosus		×	
microphyllus		×	
probalsamifera			×
sternbergii		×	
winchelli		×	
Populophyllum crassinerve	×		
hedereæforme	×		
reniforme	×		
Species 42	8	19	17
Percentage distribution	18.1%	43.1%	38.6%

Again, comparisons with existing species are instructive. If all the various forms now recognized are to be regarded as valid species, then it would appear that the genus Populus must have attained to its full development in the later Cretaceous or possibly early Tertiary time, since when it has been in a process of slow decline, or at least it has made no substantial progress. A very noteworthy feature of such comparisons appears in the somewhat abrupt increase among the Salicaceæ in common with other Dicotyledons, in the Middle Cretaceous, especially in the Dakota group. A ready explanation of this phenomenon on purely botanical grounds might be found in the facility with which hybridization gives rise to very stable forms, and it is in all probability true that such hybridization is accountable in large measure for the multiplication of forms or species in past times as it is known to be at the present day ; but to the geologist this would probably not afford an adequate reason, since he recognizes the important extent to which "accidents" as determined by exposure of strata, methods of preservation, etc., constitute very definite and often controlling factors in the number and kinds of plants which may be yielded by a given formation, in which sense Dr. Knowlton has observed "that though some types of the Cenomanian, as shown by the leaves of the Dakota group, generally remain distinct and plainly defined in the vegetation of some of the subsequent formations, the chain of evidence is not always continuous. A number of these, for example, still remain unrecognized in the Upper Cretaceous, though present in more recent strata of the Laramie or of the Tertiary. We know very little as yet of the flora of the Senonian or of intermediate stages between the Dakota and the Laramie groups. But judging from recent discoveries in Wyoming, Montana, Canada, and Vancouver Island, we have been able to recognize in the scanty materials obtained, the presence and therefore the persistence of some of the primitive or more ancient types, and it is most probable that further research will complete the evidence of the persistence and representation of the types of the Dakota group up to the Laramie, as clearly as it is observable in this flora and through the different stages of the Tertiary to the present time (Lesquereux, '92).

We are now led to ask: "What is the nature of the evidence, with respect to the particular form and value of the plant remains, upon which our knowledge of the geological succession is based?" Of the internal structure of the fossil Salicaceæ we as yet know nothing, for with the exception of a few specimens from the Pleistocene, the wood of these plants has not yet been brought under examination, and we are therefore denied one of the most definite means of distinguishing with certainty not only the various species and genera, but also the relations which the members of this group bear to one another and to other groups. That fragments of the stems of willows and poplars must sooner or later be found and brought under examination, is altogether probable, and as an essential provision for the proper recognition of the various species at such times, it is important that accurate diagnoses of existing species should be made.

The only evidence at present available for the recognition of members of the Salicaceæ, is in the remains of their leaves which are too often found in a very fragmentary condition and otherwise unsatisfactorily preserved. Recalling the extent to which hybrid and variable forms occur in this family, and the often extreme differences which may arise in the same species as shown by Ward ('88), Holm ('90, '95), Berry (: 01–: 03, : 02a, : 02b), and Penhallow (: 04), it is readily seen that the numerical distribution of these leaf forms in geological time cannot be regarded as affording an accurate basis upon which to found a knowledge of succession, and such remains can never be of more than approximate value with reference to an exhibition of the most general relations. Under these circumstances, as pointed out by Holm ('95) some years since, "a careful study of the recent flora is absolutely necessary when it is desired to identify fossil leaves with even an approximate degree of correctness. The plant must be studied as it stands amidst the surroundings to which it has adapted itself and which its leaves reflect." It is altogether probable that a more complete and detailed knowledge of the Salicaceæ would show that the present forms which are recognized as distinct species, in reality represent, in many cases, only variations of the same species.

This idea is emphasized more particularly in the case of the willows by the observation that *Salix protæfolia* has no less than four variants, or five forms in all, as presented by the generally accepted specific type and the varieties designated as *flexuosa*, *lanceolata*, *linearifolia*, and *longifolia* — forms which are all characteristic of the Dakota group, though *S. protæfolia* and *S. protæfolia flexuosa* are also found in the lower Cretaceous. We therefore find that so far as the geological evidence alone is concerned, it throws no light whatever upon the possible ancestry of these plants, it affords absolutely no clue as to their relations to other groups of plants, and it gives no very trustworthy information as to their present position in the scale of development. But when such evidence is taken in conjunction with that derived from a knowledge of the family as at present existing, the following conclusions appear to be fully justified:

(1) The Salicaceæ as a whole is an Old World family with its probable center of distribution in southeastern Europe and Central Asia.

(2) It is a family with a strong tendency to a boreal habit which has become more definitely emphasized since Tertiary time.

(3) The present tropical and subtropical members of the family, probably represent the relics of a wider dispersion in Cretaceous and Tertiary time, which have been isolated and localized as the result of more recent contraction in the family as a whole.

(4) The family at present affords strong proof of a temperate climate. In Cretaceous time it was compatible with a much warmer climate than at present, as indicated by the survival of tropical and subtropical forms; but changes more recently effected, have made its tendencies boreal rather than tropical.

(5) The family had but a feeble development in the Lower Cretaceous, but become greatly augmented in the Middle Cretaceous.

(6) It is a family which may be regarded as still in process of development.

(7) The process of evolution is chiefly expressed in the genus Salix which shows a very great increase since the Middle Cretaceous.

(8) The process of evolution is less definitely expressed in the genus Populus which shows but little advance since the Middle Cretaceous, and it may possibly be regarded as having attained the culmination of its development.

While it is impossible at present to discuss the anatomy of these plants in the light of their ancestral forms, the study of existing species may serve an important purpose as a working basis for future paleontological research in this direction, and it may eventually prove to be the key which shall unlock the door now concealing important records of the past. In this sense it is necessary to formulate a theory of possible descent as a working hypothesis, and this can be obtained only through a detailed study of the anatomy of the Salicaceæ in comparison with what has already been ascertained to represent certain laws of development in the gymnosperms. This hypothesis may be stated briefly before proceeding to a discussion of those anatomical details which may lend it support.

A comparison of the ferns, arborescent pteridophytes such as Calamites and Lepidodendron, and the arborescent types of gymnosperms and angiosperms, shows, in general terms, that the so called wood increases in proportion to the requirements of mechanical support. This latter is usually met by the disposition of the tissue in such a manner as to afford the most effective resistance to external stress, and it is therefore disposed in monostelic stems, in the form of a definite cylinder which constitutes the secondary xylem structure. It is also an essential feature of the same law, that the secondary xylem should be in all cases radially external to the protoxylem, and that its augmentation in secondary growth of the stem must always arise in radial succession.

In the polystelic ferns where the secondary xylem consists almost wholly of vessels and the wood elements are numerically subordinate, these latter are distributed among the other elements of the xylem and do not form a specialized mechanical region. Such strengthening as these plants require, is accomplished in the first instance by the sclerenchymatous bundle sheath, and secondarily by the more general conversion of the fundamental tissue into hard sclerenchyma. It is similarly

impossible to compare such plants in any direct way with the polystelic angiosperms in which the mechanical tissue generally encloses the vascular structure in a more or less definite sheath which exhibits a more or less clearly defined relation to mechanical stress. While, therefore, for the purposes of our present argument, it is impossible to introduce exact comparisons with any of the polystelic forms of stems, we must nevertheless conclude that the secondary wood, in whatever form it may be disposed, must be regarded as differentiated to meet mechanical ends as shown by Williamson ('71) in his various elaborations of the Calamitean structure and as more recently stated by White (:05); but a knowledge of the relations existing between the protoxylem and the secondary xylem requires a more critical examination in detail, in order to determine the course of development which has given to the gymnosperms and the dicotyledonous angiosperms, the peculiar structural aspects distinguishing them respectively. This will constitute the subject of a special paper at a future date, and in the meantime it will serve our present purpose to state briefly the fundamental conceptions which form the essential features of our hypothesis. In order to make our point of view more clear, it will first be necessary to state concisely what has been shown to hold true of the gymnosperms with respect to the evolution of the secondary vascular structure and its economic aspects in relation to the requirements of support, as well as its physiological *rôle* in the conveyance of nutrient fluids.

The origin of the gymnosperms in the Cycadofilices, or at least a portion of them, is now generally accepted as an established fact. The essential starting point for the evolution of the vascular cylinder is therefore to be found in the scalariform and spiral vascular elements of the Cycadofilices or their filicinean ancestors which constitute the entire vascular bundle of those plants, and which, in the gymnosperms, constitute the protoxylem structure only. The relatively greater extent to which the mechanical elements are developed in some of the Cycadofilices and in the Cycadaceæ as a whole, is in direct response to the somewhat more arborescent tendency of these groups as particularly expressed in certain genera; while the fact that they do

not in any case attain to the extreme preponderance noted in the Cordaitæ and Coniferæ, etc., is precisely in harmony with the general approximation of the Cycadaceæ as a whole to their filicinean ancestors and the lack of need for that peculiar form of mechanical support which is demanded by trees of large size, and which is provided in all the arborescent forms of the seed plants. With these statements it will be unnecessary to follow the Cycadaceæ in further detail, but rather to consider the course of events in the more arborescent Cordaitales and Coniferales where the analogy with the angiosperms is closest. It is now a well recognized fact that the protoxylem of the gymnosperms constitutes a transition zone within which peculiar and often somewhat remarkable evolutionary changes take place. The protoxylem or transition zone is a region peculiarly sensitive to the controlling influences of environment, and its response is so immediate as to give rise to structures of a very diverse nature. This has been shown to be true of the Cycadaceæ (Penhallow, :04c) to a notable extent, while it is no less prominent in the Cordaitæ, both of which groups are of a recognized primitive character among gymnosperms and stand in somewhat close relations to their Cycadofilicinean ancestors. But a very important difference exists between these two groups with respect to the survival of the protoxylem and the precise composition of the secondary wood. In the Cycadaceæ the growth of the stem in annual increments involves the complete repetition of the entire xylem structure and the formation of secondary growth in a manner which is to be met with in no other group of gymnosperms. The growths of successive years are not immediately joined to one another and therefore conterminous, but they are separated radially by very definite zones of fundamental tissue of the original cortex. In each zone of growth we recognize spiral and scalariform elements of a transitional form, together with tracheids bearing bordered pits and forming the secondary xylem. These tissue regions are disposed precisely as in the growth of the first year; they bear the same relations to one another both in position and in development, and in each case they perform the same functions as in the initial zone. From this it follows that there is a complete regeneration of the

xylem structure in all its parts, with each year of growth, and it is not unreasonable to consider that the same structural regions should be designated by the same terms wherever they may occur. In this sense, therefore, we should recognize the primary growth, as well as the secondary growth of each subsequent year, as composed in each case of protoxylem and secondary xylem. The protoxylem survives throughout the entire life of the plant.

In the higher gymnosperms as also in the Dicotyledonous angiosperms, the case is quite different. In them the rings of secondary growth are in all cases united to and conterminous with the structure of the preceding year, and under these circumstances, as well as for reasons which will again be referred to, the protoxylem experiences complete suppression and does not reappear after the growth of the first year. In this case, then, the primary growth consists of protoxylem and secondary xylem, while the secondary growth consists altogether of secondary xylem, and in this we find one of the most important structural distinctions between the Cycadaceæ and all other types of gymnosperms, bringing the former into the closest relations with their ancestral forms and removing the other gymnosperms with the Cordaitales as the basal member of the series, to a distinctly higher phylogenetic position.

In Cordaites, reduction has been developed to such an extent that the protoxylem no longer forms a constituent part of the annual rings of growth, since it is wholly confined to the growth ring of the first year where it constitutes a region of very considerable radial extent, gradually merging with the secondary xylem in such a way that there is no sharp line of demarcation between the two. Within this zone graduated transitions are a well known and remarkable feature; but it is to be noted that in all these respects there is a further removal from the ancestral forms and a distinct development along those lines of evolution which eventually issue in the characteristic structure of the higher Coniferales. As these latter are reached, it is to be observed that there is a constantly greater reduction in the radial extent of the transition zone, and the intermediate structural variations which it presents, until, eventually, it becomes

only a few elements broad, and there is an abrupt transition from spiral or scalariform structures to the tracheids with bordered pits. We may therefore consider that in all the higher Coniferales, the structural type is fixed to such an extent that evolutionary aspects are no longer presented.

The changes initiated in the transition zone relate to the evolution of the modified vessels or tracheids which constitute the bulk of the structure in the vascular cylinder. In the development of such tracheids their capacity for the movement of the transpiration current is not lost, except in special cases, but it is rather modified with reference to the total extent of the conductive tissue and the somewhat low rate at which the transpiration current is required to move. Each tracheid is provided, among the primitive forms, with bordered pits on both the radial and tangential walls through which a somewhat ready and direct transverse diffusion is provided for, while diffusion in a longitudinal direction can never be otherwise than indirect and therefore at a relatively slow rate. With an advance in organization, the bordered pits tend to disappear from the tangential walls where they survive only at the ends of tracheids or in the summer wood, the latter distribution being necessitated by the peculiar radial compression which such cells experience. It follows from this that in all the higher types of the gymnosperms, there is a greater degree of restriction imposed upon the transverse diffusion and through the latter, also a further restriction of the longitudinal diffusion. Whatever deficiency in circulation is developed through these structural alterations, compensation is provided by the great extent to which such tissue is formed; and that the tracheids effectively discharge the duty imposed upon them in this respect is manifested in their complete replacement of the true vessels of the protoxylem, as well as in the fact that those of the heart wood may resume their functional capacity for the conveyance of nutrient fluids when the sap wood becomes incapacitated through desiccation or other causes (Goodwin, '88). Such restricted movement of the transpiration current is in direct accord with the generally xerophilous character of the gymnosperms, whether this latter be correlated with absolute deficiency of water supplies or a

temperature which is so reduced as to permit of but slight absorbent activity in the roots; and so it is found that the peculiar form of the conductive tissue is really developed in correlation with the environment of the plant. But it is to be observed that the protoxylem is called upon, in the course of its development, to meet another essential factor in the life of the plant, namely, its ability to withstand external stresses of various kinds and through this the establishment of an upright position for the organism. It is quite conceivable that this requirement might be met by the evolution of a specialized form of element from the meristem without reference to the prior development of vessels, and this might be looked for in the angiosperms, but such has certainly not been the case in the gymnosperms. The somewhat slight modification, and in some senses the reduction which the vessels of the protoxylem have undergone in their adaptation to the movement of the transpiration current, has also permitted of their immediate adaptation to the purposes of mechanical support. They have therefore become more fibrous in character, while at the same time their walls have become sensibly thickened and in corresponding degrees more fully fitted to withstand stress. It is thus evident that two forms or directions of development have been combined in the same element, and it is no doubt also true that the peculiar form of the pits is in itself a direct resultant of such a combination development, since it has been shown that the bordered pit represents a localized area which has been left over in the otherwise general thickening of the wall in response to the requirements of intercellular circulation. The reduction of the bordered pit and its frequent elimination from the wall of the tracheid, especially in the summer wood, is in direct harmony with these statements and represents the relative predominance of requirements relating to circulation or mechanical support at different periods of growth and under special conditions of environment. So far as we know at present, no further modification of the tracheid than that presented in existing species is possible to the gymnosperms, and this particular line of evolution may therefore be regarded as completed in that group.

Our hypothesis as applied to the angiosperms on analogous

lines of development, is based primarily upon the idea that the well marked differentiation of conductive and mechanical tissue which is everywhere so prominent a feature of the arborescent forms, extending in a less conspicuous way to herbaceous types, cannot be secondary to and therefore derived from that special course of development which is so fully expressed in the wood of the gymnosperms; but that it must have had its origin in antecedent or contemporaneous types, and that it must in consequence represent a wholly distinct line of evolution arising in response to very dissimilar environmental conditions.

In the angiosperms, representing as they unquestionably do, a higher type of development, there is, even among their most primitive forms, a further removal from the ancestral type, and as presented by the Dicotyledons, they must be regarded as essentially occupying the same general plane of development as the higher Coniferales, inasmuch as they are all characterized by a transition zone consisting of but few protoxylem elements; and the passage from these latter to the elements of the secondary xylem, whether vessels or wood cells, is abrupt and direct. Like the higher Coniferæ, therefore, they represent types in which the structure of the transition zone is essentially fixed, and under normal conditions of development the formation of the secondary xylem is, from the first, in direct response to a fixed habit. We may nevertheless expect that under exceptional conditions of growth such as would involve reduced vigor, and also such as through an induced habit of growth would eliminate very largely the special necessity for mechanical support, there would be a more or less marked tendency in the direction of reversion to primitive structural conditions. Such reversions might be expected to show a distinct augmentation of the transition zone with the appearance of transitional forms of the anatomical elements, which would then diverge from the protoxylem in the particular directions imposed by the natural fixed habits of the genus or species as the case might be. Alpine forms of otherwise large trees might be expected to afford the most favorable material for the exhibition of such reversions in consequence of (1) the greatly reduced form and size of the plant consequent upon its unusual environment, and (2) the fact that

a dwarfed or even prostrate habit of growth no longer imposes those demands for rigid support which are from the first a prime necessity of the strictly arborescent forms. Precisely such conditions and precisely such results are to be met with in *Salix cutleri* Tuckerm., of which a more detailed account will appear on a subsequent page.

In the development of the secondary xylem of angiosperms, two distinct lines of evolution are to be observed — the one leading to the exaggerated development of vessels, the other leading to the exaggerated development of mechanical tissue, the two being balanced with respect to the relative excess of requirements on the one side or the other. Confining our attention in the first instance to the vessels, it is found that in their evolution from the elements of the protoxylem, these latter deviate more widely from a fibrous form so that their products become broader and either actually or relatively shorter, while the terminal walls often disappear altogether, thus giving rise to tubular structures of indeterminate length. The walls of such vessels are somewhat modified by secondary thickening, though relatively to their usually great breadth this is not more than is demanded by their own need for support, and it cannot be regarded as an essential factor in the strength of the organism as a whole. Like the tracheids of the Coniferae, the walls are characterized by the presence of bordered pits which differ in two very important respects from the similar markings which generally characterize the higher gymnosperms. They are always multiseriate and chiefly hexagonal, though as shown in the Salicaceæ, they may become more distant and definitely rounded; they also occur on both the radial and tangential walls. In both of these features the vessels show the survival of primitive characteristics which are only partially represented among the Cordaitales, and which indicate that the ancestral forms must be looked for among the Cycadofilices where they are of well known occurrence, or else among some other group of similar structural characteristics, but of which we have no present knowledge. Now the angiosperms are essentially all broad-leaved plants adapted to a distinctly mesophytic habit, and it is therefore to be concluded that the transpiration current not only moves with greater rapidity

as compared with the Coniferæ, but that it is of greater volume and requires a correspondingly more capacious channel; while such channels must also be direct and involve fewer impediments to free circulation in a longitudinal direction. These requirements are met by the large, transverse volume of the individual vessel; by the great multiplication of vessels so characteristic of Catalpa, Salix, Populus, etc.; by their repetition in the secondary xylem of each year's growth, and in the provision for very free longitudinal movement of fluids as expressed in the sieve-like terminal walls, or in the complete obliteration of such interposed septa. Although such vessels retain their capacity for the conveyance of the nutrient fluids for a long time, *i. e.*, several years, they eventually become functionless, often through the formation of extensive thyloses as in the Catalpas, members of the Salicaceæ, Quercus, etc., and in general terms the functional capacity of the vessels cannot be restored when so lost, while under certain circumstances, the development of thyloses may assume a definitely pathological aspect (Watt, :01). From the observations thus far made, it is evident that the particular evolution of the protoxylem which results in the formation of such vessels, provides elements which are solely concerned in the movement of the transpiration current, and which have, as it were, appropriated this function in such an exclusive sense as to eliminate it from all other structural elements of the xylem, so that these latter are thereby left free to develop in the most responsive way under the special influence of other requirements.

We may now ascertain the special features which serve to distinguish the second course of evolution from the protoxylem, already referred to. The excessive development of the conductive tissue tends to diminish the general strength and call for the formation of purely mechanical elements to an extent otherwise unnecessary. This factor operates, therefore, to emphasize the divergence of the two lines of structural evolution, giving greater prominence to the conductive elements on the one hand as already shown, and on the other hand to the mechanical elements. Certain of the protoxylem elements, otherwise potential vessels, are diverted in growth, and instead of expanding, they contract with a correspondingly greater development of the secondary wall, and assume a strictly fibrous form. This necessa-

rily leads to the greater simplification of the pits which rarely retain the bordered form but become simple perforations and commonly disappear altogether. Concurrently with these changes, the progressive increase in the thickness of the wall eventually leads to a more or less complete obliteration of the original cell cavity; and while all these varied changes have a profound bearing upon the ultimate strength of the general structure, they at the same time operate to eliminate completely even such slight capacity for conduction of fluids as the elements may have had in their earlier stages of development.

The hypothesis as thus presented, is suggested at the present time in view of the many facts which have come under observation during the progress of studies bearing more particularly upon the anatomy of the Coniferales as elsewhere recorded (Penhallow, :04c), and because of the need of some working basis from which we may view the anatomy of the Salicaceæ, and upon which we may erect a possible point of departure for an interpretation of their phylogeny. The first real test of the validity of this hypothesis will be made on the basis of data to be derived from a study of the Salicaceæ as recorded in subsequent pages. If it proves to have the support of observed facts it will then be necessary to supplement it with the further hypothesis that the angiosperms as a whole had their origin in some generalized type, possibly identical with or at least nearly related to the Cycadofilices; and in any event we can hardly agree with the suggestion of De Vries (:05) that the Monocotyledons "are obviously a reduced branch of the primitive Dicotyledons," since our own investigations not only fail to lend support to such an idea, but they tend to establish evidence to the contrary, and to the effect that while the two may possibly have had their starting point in a common, generalized type, they nevertheless represent two distinct lines of descent. On the basis of such a hypothesis, we should reasonably expect to find in the early Mesozoic and Permian, and possibly even in the later Carboniferous, transitional forms which would carry the angiosperms back to some of the later but less highly specialized types of the Cycadofilices.

(*To be continued.*)

DEVELOPMENTAL STAGES IN THE LAGENIDÆ.

JOSEPH A. CUSHMAN.

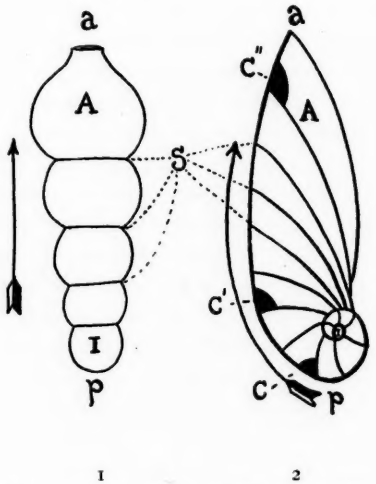
THE Foraminifera present certain characters which make their study different from that of almost any other group of the animal kingdom. They are unicellular animals, but secrete a shell which in many cases has a considerable degree of complexity and shows marked stages in development. Their geological history is very long, for representatives are found in the Cambrian sedimentary rocks and more or less in intermediate horizons to the present time. At present, the Foraminifera are found, as a rule, in the deep waters of the oceans and extending toward the shores. Some twenty or more of the species occur as pelagic forms. In these animals the intermediate steps between extreme generic and specific forms are so well filled in, even in the living species, that some authors have regarded them all as simply variations of a single species. This is altogether too extreme a view. Intermediate species may be expected when the habits, environment, and reproductive characters of the animals are taken into consideration.

That the laws of development enunciated by Professor Alpheus Hyatt may be applied to this group, is shown in the following discussion. These laws have hitherto been applied only to groups of the Metazoa but as will be shown in the present paper they are equally applicable to another group of the animal kingdom, the Protozoa.

In tracing the development of Foraminifera where young individuals can be obtained, the relations are usually made out with ease. In the absence of young individuals the most reliable method is the study of sectioned specimens, since many species which are coiled, cover all traces of the younger portion externally by their later growth. Sectioning, in many cases, is the only method by which, from adults, the characters of the early growth may be seen in their true relations.

DEFINITION OF A FEW TERMS.

The following terms as defined, some of which are new, are convenient in the description of the structure of the shell of Foraminifera. The succeeding divisions of the shell are usually spoken of as chambers, the one first formed being the initial chamber (*I* in Figs. 1 and 2) and the last one built in any given specimen, the anterior chamber (*A*). The initial chamber which will be shown to have a decidedly phylogenetic bearing in the group is here given a distinctive name — the *proloculum*—to correspond with the term applied to the embryonic shell of other groups already worked out in the Metazoa. The ends of the shell as a whole are called anterior (*a*) and posterior (*p*). The walls of the chambers are called anterior and posterior walls according to their individual position in relation to the direction of growth. The line of contact made by the joining of a succeeding to a preceding chamber is called a suture (*S*). In coiled forms the outer border formed by the sum of the distal portion of the walls of succeeding chambers is called the peripheral margin. The angle between the suture and the distal wall of the next succeeding chamber in coiled forms is called the angle of curvature for that portion of the peripheral margin. These angles are shaded at *C*, *C'*, *C''*, to show the decided differences that the angle may assume.

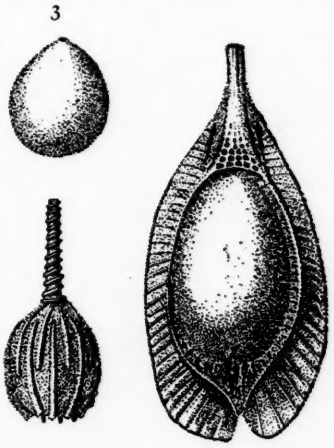


1 2

FIG. 1.— Nodosaria. FIG. 2 — Uncoiled form of Cristellaria. *A*, anterior chamber; *I*, initial chamber or proloculum; *a*, anterior end; *p*, posterior end. Arrows show the direction of growth; shaded portions indicate the angle of curvature at *C*, *C*,' *C''*; *S*, sutures.

DEVELOPMENT OF TYPICAL SPECIES OF VARIOUS GENERA.

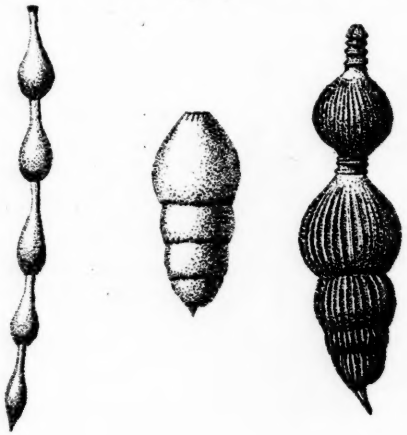
Lagena.— This genus represents the simplest condition seen in the family under discussion. In its geological history it can be traced from the Silurian to the present time. It is monothalamous or single-chambered (Fig. 3). The species very commonly develops a neck at the anterior end (Figs. 4, 5). The variation in forms of ornamentation is very remarkable and includes costæ, reticulate patterns, knobs, and bosses or broadly expanded wings of shelly material, but the underlying character of the chamber is always that of a simple flask-like form or a modification of it. This simple chamber represents the completed development of this genus, which is the only one of the family that has the single-chambered character. As it is the simplest form in the family and as all the other genera of the family start off with a simple chamber which is comparable to it, Lagena may be taken as the radical from which other genera of the family may be derived.



FIGS. 3-5.— Three species of Lagena showing the great differences in ornamentation that are found in the group. Fig. 3, *Lagena globulosa* Montagu, a smooth type; Fig. 4, *L. salcata* W. & J., var. *interrupta* Williamson, a costate type; Fig. 5, *L. formosa* Schwager, a type with expanded wing-like growths. (Figures after Brady.)

Nodosaria.— This genus in its typical form consists of a linear series of Lagena-like chambers, the posterior wall of each newly added chamber overlapping the anterior wall of the preceding one. The initial chamber or proloculum is comparable in character to the adult Lagena but the addition of the second chamber in Nodosaria shows that it is developing beyond the single-

chambered Lagena condition. The succeeding chambers add no striking characters in development further than that given by the second except in features of ornamentation which is a secondary character. The chambers of the linear series may be more or less closely overlapping (Figs. 6, 7) and this character



6 7 8

FIGS. 6–8.—Three species of Nodosaria showing the difference in the amount of overlapping, and in Fig. 8 the Lagena-like last chamber. Fig. 6, *Nodosaria pyrula* d'Orb.; Fig. 7, *N. radicula* Linn.; Fig. 8, *N. scalaris* Batsch (Figures after Brady.)

of overlapping may vary with the age of the individual as shown in progressively added chambers of *Nodosaria scalaris* var. *seperans* Brady (Fig. 8). They may also be variously ornamented according to the species but the linear series of chambers is always the essential character. Very often the last-formed or final chamber is more distinctly separated from the preceding ones and is decidedly Lagena-like (Fig. 8). Therefore at the end of growth representing old age or senescence, a chamber may occur which is closely comparable to the first stage of development in the young of the same individual or to the simpler genus Lagena. The stages of development of Nodosaria from young to old age may be expressed by a formula using the initial letters of the genera represented, as L + N + L.

Cristellaria.— The initial chamber or proloculum of Cristellaria, as in the other genera of the family, is simple and Lagena-like (Pl. 1, Fig. 6). The second chamber is added obliquely (Pl. 1, Fig. 7), as in some species of Nodosaria, and at this stage simply reveals the fact that it will not be a Lagena nor any of the straight Nodosarian forms. The third chamber of Cristellaria adds a decidedly new character. Instead of continuing on as in Nodosaria, it extends back on its inner margin so as to come in contact with the proloculum or initial chamber initiating the feature of coiling (Pl. 1, Fig. 8). In Cristellaria this coiled character is maintained throughout further growth in typical species as in Figs. 9, 18, 19. In further growth the shell may take on a flattened form as in *Cristellaria compressa* d'Orb., or may later take on a loose-coiled, or straight form of growth as in the species *C. siddalliana* Brady (Fig. 21) and *C. tenuis* Bornemann (Fig. 12) which are at present included in the genus. The typical Cristellaria is marked by the coiled form as the acme of its development (Figs. 18, 19), with a resulting close-coiled form throughout its life history beginning with the third nepionic chamber.

As with Nodosaria, a formula may be made to represent the stages in development. In Cristellaria it is the third chamber which is the determinative one, and the formula for the close-coiled form (Fig. 18) would be, Cristellaria = L + N + C. The absence of repetition of any letter in the formula indicates progressive development as a coiled form, as no senescence is seen in the form or arrangement of the chambers in typical species which are close coiled in the adult.

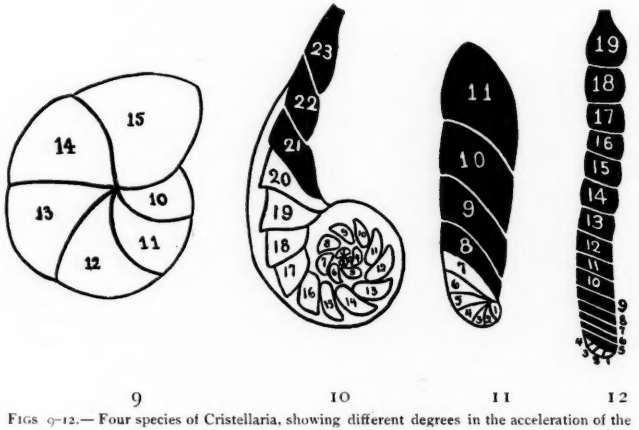
Cristellaria as at present recognized contains species showing excellent differences in the degree of acceleration of development. In such species as *C. articulata* Reuss (Fig. 9), the close-coiled character after being taken on, extends throughout the succeeding life history. In others, as *C. siddalliana* Brady (Fig. 10), the main part of the shell is close-coiled but towards the end of its growth there is an uncoiling seen in the last three chambers of this specimen. This is brought about by the failure of chamber 21 to extend back to the preceding coil and the continued shrinking away of the next-formed chambers, 22 and 23.

	Marginulina	*Cristellaria*	*Nodosaria*	*Polymorphina*	*Dimorphina*
Ephebic	5	9	13	17	21
Neanic	4	8	12	16	20
Nepionic	3	7	11	15	19
Embryonic	2	6	10	14	18
			1 *Lagena*		

PLATE 1.

The figures given show the ontogeny of representative genera of Lagenidæ, arranged to show comparative stages in development. 1, Lagena, the primitive radical; 2–5, stages in development of Marginulina; 6–9, Cristellaria; 10–13, Nodosaria; 14–17, Polymorphina; 18–21, Dimorphina; the embryonic stage, the proloculum, is represented in the lower row and may be compared to Lagena The nepionic, representing the first two chambers in the next row above, may be compared to Nodosaria. In the neanic shown in the third row the true generic characters are definitely taken on at least as regards progressive characters.

In uncoiling as is shown in Fig. 2, there is a decided change in the angle of curvature from an acute angle gradually to an obtuse one. This seems to be the rule in the stages by which a straight growth is produced from a coiled one as is shown again in Figs. 11 and 12. In *C. schlœnbachi* Reuss (Fig. 11), the uncoiled character is early taken on until on an average only the first six to eight chambers are coiled, while the succeeding chambers which constitute the major part of the whole growth, are



9 10 11 12

FIGS. 9–12.— Four species of Cristellaria, showing different degrees in the acceleration of the character of uncoiling. Blackened chambers show the extent of the senescent uncoiled portion. Fig. 9, *Cristellaria articulata* Reuss; Fig. 10, *C. siddalliana* Brady; Fig. 11, *C. schlœnbachi* Reuss; Fig. 12, *C. tenuis* Bornemann. (Figures adapted from Brady.)

uncoiled. Thus the senescent character of uncoiling in this last species is more accelerated in its development than in *C. siddalliana* as it originates much earlier in the ontogeny or life history of the individual. In such a species as *C. tenuis* Bornemann (Fig. 12), the coiled portion is usually limited to the first four chambers, while the last fifteen or more are uncoiled. Other specimens of this species show fewer chambers than that figured. This species is then, even more accelerated in development, for the senescent character is so accelerated that it includes four fifths of the entire number of chambers. In the complete return to the straight Nodosarian growth, as shown in the last few chambers of this species, there is a return to a right

angle in the angle of curvature if it may be so called. In the entire development from the right-angled condition in the Nodosarian young, there is a change gradually to an acute, then a right, next an obtuse, and finally back to the right angle again. This then represents the mechanics of the uncoiling. The character of uncoiling in these four species of Cristellaria is represented in Figs. 9–12, in which the black chambers represent the portion showing senescent uncoiling. The white portion shows the extent of the coiled development.

Marginulina.— The first three chambers in the specimen of Marginulina figured (Pl. 1, Fig. 4), are exactly comparable to the same chambers of Cristellaria (Pl. 1, Fig. 8). The first chamber is Lagena-like, the addition of the second gives the oblique Nodosarian form, and the third is seen to be truly Cristellarian. The formula thus far would be as in the preceding, L + N + C. The fourth and fifth chambers in this specimen of Marginulina, however, present a new feature; they fail to extend back to the initial one, but strike off at a tangent showing the incipient stage of uncoiling. The chambers as built, continuing in the line or direction initiated by the fourth chamber, form a Nodosarian growth and the adult therefore may be represented by the formula, Marginulina = L + N + C + N. This is shown in Fig. 14 in section, and in Fig. 13 from the exterior.

13 14

FIG. 13.— *Marginulina ensis* Reuss, showing the main portion of the growth uncoiled.
FIG. 14 — Section through median line of *Marginulina glabra* d'Orb.

In certain cases in old age the last-formed chamber is less closely overlapping than the preceding and therefore takes on a form very much like Lagena. In Marginulina, representing this last chamber in the formula we have, Marginulina = L + N + C + N + L. This shows a complete cycle of stages seen in progressive and typical sen-

escent or regressive development. Such forms as that figured and the majority of species usually classed under Marginulina are not intermediate between Nodosaria and Cristellaria as is commonly stated, but are truly senescent species derived from Cristellaria and resulting from acceleration of development and the shoving back of the Cristellarian character to the early stages in development.

Polymorphina.—The proloculum or initial chamber in Polymorphina as shown in Fig. 15, is here also simple, like Lagena, as in the previous genera. The second chamber (Pl. 1, Fig. 15) is added in the same manner as in Nodosaria and in the second stage in all its visible characters Polymorphina apparently belongs to that genus. The addition of the third chamber (Pl. 1, Fig. 16) initiates a new character in the line of development. It continues back over the preceding one to the proloculum as in Cristellaria but is added in a different manner being so placed that the aperture faces the line of the median axis. This generic character may be represented by P and the formula for the genus may be expressed as follows: Polymorphina = L + N + P. The fourth chamber also extends back to the initial chamber (Pl. 1, Fig. 17) but is added on the opposite side from the third with its aperture facing and occluding that of the third, and this character continues throughout further growth to the adult. This is then a progressive form and after its Nodosarian second stage, starts a new line of development which at once places it in a different group from Cristellaria and Marginulina.

FIG. 15.—Section through median plane of *Polymorphina compressa* d'Orb. After Flint.

Dimorphina.—In this genus the early stages up to the fourth chamber (Pl. 1, Fig. 20,) are exactly as in Polymorphina and may be represented by the same formula, L + N + P. If the animal had died at this stage it would be described as Polymorphina. After this stage, however, a quite different mode of growth is assumed. Beginning with the fifth chamber, suc-

ceeding chambers are arranged in a linear series and are therefore Nodosarian in character. The formula for the adult would be, Dimorphina = L + N + P + N. The last chamber is often more or less free and like Lagena. The formula for the completed growth including this gerontic character will then be, Dimorphina = L + N + P + N + L. Dimorphina is therefore a senescent genus having as its basis the three progressive characters of Polymorphina and in senescence has, by retracing in inverse order, attained in the last chamber to a condition comparable to that seen in the proloculum, or in other words to Lagena. Having completed the cycle, such forms evidently have attained completion along certain lines of development and no new forms can originate from this senescent type except in regard to minor changes in character of ornamentation which are recognized as specific and not generic in value.

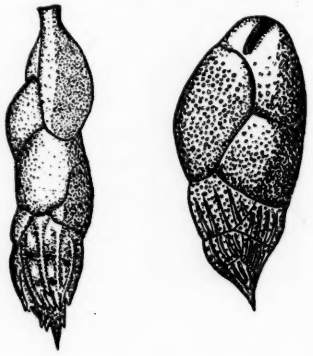
Senescent Characters.

Characters showing typical senescence are frequent among the Foraminifera and illustrate in simple terms conditions similar to those found in many other groups of the animal kingdom. The simplest of these senescent characters is the loss of ornamentation. The ornamentation of this group is shown mainly by elevated ridges, by tubercles, or by spines. Examples of the loss of these will be given. As found by Hyatt in Cephalopoda, the uncoiling of forms, which in their early development were close-coiled, is a decided feature of senescence. Such cases are seen in their simplest terms among the Foraminifera. As shown by Beecher, one of the characters apt to appear in the decline of a group is a peculiar spinose or extravagant growth, "wild" growth, as it is sometimes called in the Foraminifera. Certain senescent genera of Foraminifera show this character exceptionally well. One of the surest indications of senescence is a return to the simpler conditions seen in the young of the same individual and in the adults of more primitive forms. Excellent and at the same time very simple cases of this are seen in Dimorphina and in Dentalinopsis. The Foraminifera as uni-

cellular organisms seem to present the simplest conditions and examples for the expression of the various laws of development that can be found anywhere in the animal kingdom.

LOSS OF ORNAMENTATION.

Ridges. — In a specimen of *Uvigerina angulosa* Williamson, var. *spinipes* Brady (Fig. 16), the early chambers have definite raised costæ or ridges running generally parallel to the axis of the growth of the shell. In later growth this character becomes less pronounced and in the last five chambers which by measurement represent more than half of the growth, is entirely wanting, and the chambers are perfectly smooth. Although not included in this family, *Bulimina subornata* Brady is figured here for comparison. It shows in much the same manner (Fig. 17) the costate early growth and the gradual disappearance and final loss of costation in the old age of the individual.



16 17

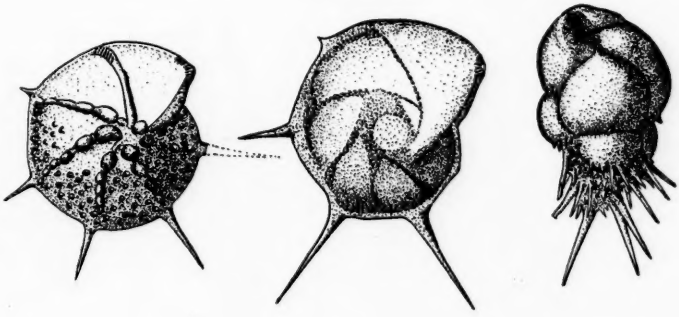
FIG. 16.— *Uvigerina angulosa* Williamson, var. *spinipes* Brady, showing loss of ornamentation in senescence.

FIG. 17.— *Bulimina subornata* Brady, showing similar senescence. (After Brady.)

Tubercles.— In *Cristellaria echinata* d'Orb. (Fig. 18), the early growth is marked by rows of bead-like tubercles over the sutures, while the intermediate space is covered with hemispherical granules. In later growth these scattered granules are limited to the peripheral portion and on the last two chambers are entirely wanting, so that the surface of these chambers is smooth. The rows of bead-like tubercles also disappear in old age and pass into a smooth ridge. Similar conditions are found in various groups of the Mollusca, especially in certain of the fossil Trigonias. In such forms the costæ break up into knobs and bosses in development, and later in the old age of

the individual again resume a costate condition by the merging together of the tubercles.

Spines. — In the preceding species, *C. echinata* d'Orb. (Fig. 18), the loss of spines is a very evident character in senescence.



18 19 20

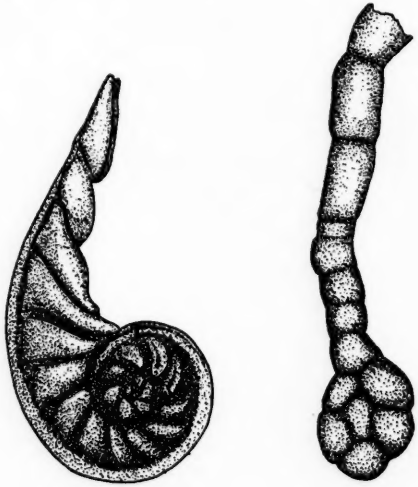
FIG. 18 — *Cristellaria echinata* d'Orb, showing loss of ornamentation in senescence.
FIG. 19 — *C. calcar* Linn., showing loss of spines.
FIG. 20 — *Bulimina aculeata* d'Orb., showing similar loss of spines (After Brady.)

In the median portion of growth the peripheral spines at the sutures are long, at least equalling the length of the chamber on the peripheral margin. The third from the last is shorter and the last two spines decrease progressively in size, the last one being very short, while at the last suture no spine at all is developed. Much the same condition of affairs in regard to the reduction and loss of spines is seen in *C. calcar* Linn. (Fig. 19), in which, however, the spines do not coincide with the suture lines. Another excellent example, although not in the same family, is that presented by *Bulimina aculeata* d'Orb. (Fig. 20). Here the early growth is marked by well developed spines. As growth progresses, the spines of successively added chambers are not so greatly developed. Toward the later growth, traces of them are seen in the very reduced spines at the posterior angles and on the last-formed chambers they are lacking, and the chambers are perfectly smooth.

These examples of loss of ornamentation as a character in senescence are exactly comparable to cases already worked out

by others in the Cephalopoda, Pelecypoda, Gastropoda, and Brachiopoda and they are seen in still other groups.

Uncoiling.— Cristellaria siddalliana Brady (Fig. 21) shows an excellent case of uncoiling not carried to an extreme. The



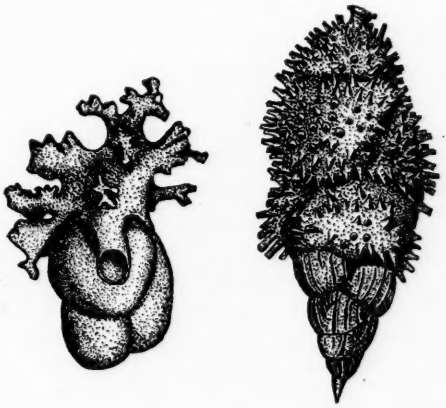
21 22

FIG. 21.— *Cristellaria siddalliana* Brady, showing uncoiling in last few chambers.
FIG. 22.— *Trochammina lituiformis* Brady, showing uncoiling carried to an extreme.

early chambers are close-coiled and this feature continues until the last few chambers. Here there is a distinct change and an uncoiled form is produced as shown in the figure. This uncoiling is only seen in well advanced specimens that show old age characters. Other examples of uncoiling in Cristellaria have already been given (Figs. 11, 12). Although outside of this family, *Trochammina lituiformis* Brady is figured (Fig. 22) to show the character of uncoiling carried to an extreme. The early chambers make a little more than a single volution, while the succeeding growth is uncoiled. In old age specimens, this character may be carried to a greater extent than is shown in Fig. 22. In this species in contrast to the preceding, the majority of the chambers form the uncoiled portion of the shell. Such examples are exactly comparable to Baculites or Lituites

among the Cephalopoda or to Vermetus or Magilus among the Gastropoda.

Spinose or "Wild" Growths.— In Polymorphina and Sagrina of this family the last chambers are often peculiarly different from the preceding ones. In *Polymorphina orbignyii*, as figured by Brady, Parker, and Jones (*Trans. Linn. Soc. London*, vol. 27, p. 244, pl. 42, fig. 38c) the last chamber is marked by a peculiar fistulose growth, greatly differing from the preceding regular chambers of the species (Fig. 23). Such growths are



23 24

FIG. 23.— *Polymorphina orbignyii* with peculiar fistulose growth in senescence.
FIG. 24.— *Uvigerina aculeata* d'Orb. with "wild" growth. (After Brady.)

not infrequent in various other genera. Corresponding "wild" growths appear in certain species of Cristellaria. In *Uvigerina aculeata* d'Orb. (Fig. 24) similar characters appear. This species in its younger development has simple longitudinal costæ. Later, however, there is a thickening by addition from the outside and the last chamber is covered with a decidedly spinose development totally different from the previous ornamentation. This spinosity may continue, extending progressively posteriorly until it envelops the whole shell, covers the preceding chambers, and hides all traces of the typical earlier ornamentation. These growths seem to be best regarded as senescent charac-

ters. Such a decided change in method of growth, with an increase in the thickness of the shell without corresponding increase in the number of chambers, may be compared in a general way to the building up of tissue in the old age of Brachiopoda and Mollusca where there is no increase in size of the living chamber but frequently a decrease. It may be more closely compared to similar conditions which appear in the Gastropoda for example in the several Eocene species of Calyptraphorus where by reflection of the mantle in later growth a callous develops which hides the previous sculpturing.

RETURN TO SIMPLER CONDITIONS.

Dimorphina.— In this genus, the development of which has already been noted, there is a return to a straight uniserial growth in the later chambers. This was expressed by the formula L+N+P+N+L. It is a true return to the Nodosarian and Lagena characters seen in the progressive development of the first two chambers. The biserial Polymorphine character in Dimorphina is accelerated so that it may appear in but two chambers including the third and fourth and a return to the uniserial condition is then taken on in the fifth. This return to the simpler Nodosarian condition, seen in the young of the same individual and again as the acme of development in an ancestral type, Nodosaria, can be regarded only as a truly senescent character and the genus Dimorphina a senescent one derived from Polymorphina.

FIG. 25.— *Dentalinopsis subtriquetra* Reuss, showing return to circular cross section in the last-formed chamber. (After Reuss.)

Dentalinopsis.— In this genus (Fig. 25), the early chambers are uniserial like those of Nodosaria. At first they are circular in cross section but soon become triangular or polygonal. At this point the species which have this character as their highest development are classed under the genus Rhabdogonium which is characterized by angular section in the adult. The formula for Rhabdogonium would be L + N + R.

Senescent forms have been found among the fossils and to such forms Reuss has applied the generic name Dentalinopsis. In species of this genus the later growth instead of being triangular reverts to its earlier circular cross section and becomes truly Nodosarian. Reuss noted the generic value of this senescent character, although his genus has not always been recognized by later writers. The last-formed chamber may be more free and distinctly Lagena-like, thus completing the reversion in senescence. The formula for a specimen which has the Lagena-like last chamber would be L + N + R + N + L, showing its definite regressive senescence.

STUDIES ON THE PLANT CELL.—VII.

BRADLEY MOORE DAVIS.

SECTION V. CELL ACTIVITIES AT CRITICAL PERIODS OF ONTOGENY IN PLANTS (*Continued*).

5. APOGAMY.

APOGAMY is the suppression of the sexual act and the development of a succeeding generation asexually. The term was first proposed by De Bary in 1878, following Farlow's ('74) discovery of the phenomenon in *Pteris cretica*. The succeeding generation may arise in one of two ways: (1) by the development of an unfertilized egg or gamete which is termed parthenogenesis, or (2) by some form of vegetative outgrowth from the sexual plant, a process which has been called vegetative apogamy. We shall not attempt to give a detailed account of apogamy in the plant kingdom but will confine ourselves chiefly to the consideration of a few detailed studies of recent months which have taken up the cell problems concerned. The cell problems naturally treat of the processes which may be substituted for the sexual act in ontogeny and the fundamental problems of the behavior of the chromosomes under these conditions.

Parthenogenesis has been known for many years among the thallophytes which furnish illustrations in a variety of groups. In the algæ we have the well known examples of *Chara crinita*, Cutlaria, Dictyota, some species of Spirogyra and Zygnema, and a number of types in the lower Chlorophyceæ and Phæophyceæ whose motile gametes will germinate like zoöspores should they fail to conjugate with one another. The recent studies of Williams (:04b) on Dictyota give the only observations which have been made on nuclear activities during the parthenogenetic development of eggs in any algal form and will be considered presently. The fungi furnish beautiful illustrations of partheno-

genesis in the Saprolegniales. Trow (:04) believes that some of these forms are sexual but there can be little doubt that the group as a whole is generally apogamous. There is probably much apogamy in the Ascomycetes and an almost entire suppression of sexual organs in the Basidiomycetes but no clear instance of parthenogenesis (*i. e.*, a development from a cell whose morphology is unquestionably that of an egg) is known in either of these groups.

Parthenogenesis is not known in the bryophytes and pteridophytes excepting for Marsilia (Shaw, '97; Nathansohn, :00). Although there is much apogamy in the pteridophytes, especially in the leptosporangiate Filicales, the new generation generally develops as a bud-like outgrowth on the prothallus (vegetative apogamy). There have been no nuclear studies on the parthenogenetic Marsilia but an interesting preliminary account has appeared announcing nuclear fusions in the apogamous development of Nephrodium (Farmer, Moore, and Digby, :03).

Parthenogenesis is now known in the spermatophytes for *Antennaria alpina* (Juel, '98, :00), several species of Alchemilla (Murbeck, :01a, :01b, :02; Strasburger, :04c), *Thalictrum purpurascens* (Overton, :02, :04), Gnetum (Lotsy, :03), a number of forms of Taraxacum (Raunkiaer, :03; Murbeck, :04), several species of Hieracium (Ostenfeld, :04a, :04b; Murbeck, :04), *Wikstrœmia indica* (Winkler, :05), and is suspected for Ficus Treub, :02) and *Bryonia dioica* (Bitter, :04). A number of cases of polyembryony were formerly considered examples of apogamy but are now known to be developments from the nucellus and consequently vegetative buds of sporophytic origin and entirely independent of gametophytic activities. The best known of these forms are Funkia, Cœlebogyne, Citrus, Opuntia, and *Alchemilla pastoralis*. Vegetative apogamy is illustrated in the development of embryos from antipodal cells as in *Allium odorum* (Tretjakow, '95; Hegelmaier, '97) or from the cells of the endosperm as in Belanophora (Treub, '98; Lotsy, '99). Synergids have been reported to form embryos in a number of forms but many of these have proved to be cases in which the synergid is fertilized by a sperm nucleus and not examples of apogamy. However, synergids are known to develop embryos apogamously

(or parthenogenetically if the antipodal be considered the homologue of an egg) in *Alchemilla sericata* (Murbeck, :02). A summary of the various types of vegetative apogamy, parthenogenesis, and sporophytic (nucellar) budding, supplementing a list of Ernst (:01) is given by Coulter and Chamberlain (:03, p. 221).

We will now take up the few investigations which consider the cytological details of parthenogenesis. That of Williams (:04b) on Dictyota is the only one treating of a lower type. It seems probable that parthenogenesis in Dictyota is in no sense normal and would not lead to mature plants, since the germination of unfertilized eggs in the cultures of Williams presented many irregularities. The spindles instead of being formed from asters with centrosomes are intranuclear in origin, multipolar, and very irregular in their form. As a result the 16 chromosomes become scattered and a cluster of daughter nuclei is formed containing varying numbers of chromosomes, sometimes one and sometimes several. It is clear in Dictyota that the fertilization of the egg results in the development of an aster with a centrosome which exerts a directive influence in mitosis preventing a scattering of the 32 chromosomes and conducting the mitosis in a normal fashion. Williams does not believe that the centrosome is introduced as an organized structure into the egg by the sperm but that it is formed *de novo* as a result of the increased metabolic activities present in the fusion nucleus as compared with that of the unfertilized egg.

There have been several important studies on parthenogenesis in the spermatophytes. Some of these papers while establishing the facts of parthenogenesis in various forms, give no details of nuclear history or behavior of the chromosomes. But the studies of Juel (:00), Overton (:04), and Strasburger (:04), present some very interesting data on the cytological features of parthenogenesis in *Antennaria alpina*, *Thalictrum purpurascens*, and several species of Alchemilla.

Several recent papers indicate that parthenogenesis may prove to be general in certain genera or even characteristic of large groups and therefore a far more widespread phenomenon than has been supposed. Raunkiaer (:03) (abstract in English in *Bot. Centralb.*, vol. 93, p. 81, 1903) proved by cutting off the

tops of young flowers that several species of Taraxacum produced normal seeds apogamously and concluded that the embryo must develop parthenogenetically since Schwere, in 1896, traced its origin from the egg. Ostenfeld (:04a, :04b) from failure to find pollen on the stigma of Hieracium and failure to make it germinate in a number of solutions, was led to try similar experiments to those of Raunkiaer in cutting off the anthers and stigmas of flowers. He found that a large number of species of Hieracium were able to set seed apogamously and he believed parthenogenetically but histological investigations were not made to establish the last point. The experiments of Raunkiaer and Ostenfeld are interesting as showing how a form by virtue of its parthenogenetic habits might become segregated and quite removed from the probability of hybridization. Murbeck (:04) in a short paper announced that the embryos in Taraxacum and Hieracium, developing from flowers whose stamens were cut out (as in the experiments of Raunkiaer and Ostenfeld) actually do develop from the egg cell and are therefore parthenogenetic. Murbeck also failed to find pollen tubes in the ovules where pollen had been applied to the stigma. Winkler (:04) reports that *Wikstrœmia indica* matures very little perfect pollen and produces its seeds apogamously, as proved by experiment. The embryos are stated to develop parthenogenetically from the egg but no details are given in this preliminary paper of the chromosome history. This group of contributions while very interesting, presents no data on the fundamental problems in a cytological explanation of parthenogenesis.

Murbeck (:01a) concluded for Alchemilla that true tetrads were formed previous to the differentiation of the embryo-sac but nevertheless found evidence that there were no reduction phenomena so that the nuclei within the embryo-sac contain the sporophytic number of chromosomes. Murbeck's evidence of tetrad formation was not satisfactory and in the light of recent studies of Strasburger (:04c) cannot be accepted. His view was, however, correct that there is no reduction of the chromosomes in the formation of such embryo-sacs as produced parthenogenetic embryos.

Juel (:00) gives a critical comparison of the development of

the embryo-sac in the parthenogenetic *Antennaria alpina* with *A. dioica* whose ovules are normally fertilized. In *A. dioica* the embryo-sac is one of a group of four cells (tetrad) which are formed through two successive mitoses (heterotypic and homotypic) showing the characteristic features of sporogenesis. A clear stage of synapsis precedes the first mitosis. The type of embryo-sac development in this form is then entirely normal. Not only are tetrads suppressed in the parthenogenetic *Antennaria alpina* but there is no trace of the heterotypic and homotypic mitoses in the embryo-sac. The number of chromosomes is very large (about fifty) and evidently the same as is found in other periods of the life history. There is then no reduction of the chromosomes during the formation of the embryo-sac in the parthenogenetic species and the egg and other nuclei in this structure have consequently the sporophytic number. There is no need of fertilization to bring the egg to a condition when with respect to chromosomes it is prepared to develop a sporophyte embryo. Juel (: 04) notes certain peculiarities in the development of the embryo-sac of *Taraxacum officinale*. Tetrad formation is reduced to a single mitosis and this is not heterotypic, since there seems to be no reduction of the chromosomes. Details are not given.

Overton (: 04) finds normal reduction phenomena in the pollen mother-cell of *Thalictrum purpurascens* which establishes the number of chromosomes to be 24 for the sporophyte and 12 for the gametophyte generations. These mitoses are thoroughly typical of sporogenesis being preceded by a synapsis stage. The development of the embryo-sac is of two types. In some cases a tetrad of four megaspores is formed from a megaspore mother-cell. The nucleus of this cell passes through a synapsis and the first mitosis is heterotypic showing the reduced number of chromosomes. The lower cell of the tetrad becomes the embryo-sac. But many embryo-sacs pass through a different history. There is no heterotypic mitosis and no reduction of the chromosomes which remain 24 in number. Thus in some ovules the mitoses of sporogenesis are omitted and true tetrads are not formed, with the result that the embryo-sac contains nuclei with the sporophyte number of chromosomes (24) in

place of the gametophyte (12). The details of the nuclear history in these embryo-sacs have not been followed but it is plain that their eggs have the requisite number of chromosomes to develop sporophyte embryos parthenogenetically. The varying proportions of parthenogenetically developed seeds which may be found on plants of *Thalictrum purpurascens* indicate that the suppression of normally developed embryo-sacs is not very firmly established in this form.

We now come to a recent paper of Strasburger (:04c) which is the most important contribution to the subject of parthenogenesis that has yet appeared. Strasburger studied a number of species of Alchemilla from the section Eualchemilla, the group which formed the subject of Murbeck's important discoveries. Most of the forms develop pollen in a normal manner and Strasburger was able to follow reduction phenomena in this process without difficulty. The nucleus of the pollen mother-cell passes through a synapsis followed by a heterotypic mitosis in which the structure of the chromosomes as bivalent elements is apparent. The bivalent chromosomes are in the reduced (gametophytic) number. Similarly Strasburger found that some species (*e. g.*, *Alchemilla pentaphylla*, *gelida*, and *grossidens*) formed embryo-sacs in a normal manner with the presence of a tetrad and a characteristic reduction division (heterotypic). But the development of the embryo-sac in apogamous species (*e. g.*, *Alchemilla speciosa*, *splendens*, and *fallax*) cuts out the two mitoses of sporogenesis and no tetrads are formed. The nucleus of the megaspore mother-cell emerges from synapsis with the sporophyte number of chromosomes and the first division which follows is a typical mitosis and not heterotypic. The embryo-sac then comes to contain a group of nuclei with the sporophytic number of chromosomes in place of the gametophytic and a parthenogenetic development of the egg takes place. Strasburger regards the parthenogenetic tendencies of Eualchemilla as associated with excessive mutations among these forms through which sexual processes are becoming displaced by apogamous methods of reproduction.

This clear evidence that the cause of parthenogenesis in Antennaria, Thalictrum, and Alchemilla lies in the suppression

of chromosome reduction during the formation of the embryo-sac seems to offer an explanation of other examples of apogamy presented by the embryo-sac. Thus apogamous developments of embryos from synergids as in *Alchemilla sericata* (Murbeck, : 02) or from antipodals as in *Allium odorum* will not seem strange if reduction processes are suppressed in the production of an embryo-sac and its nuclei retain the sporophyte number of chromosomes. Such nuclei have in them the same potentialities of development as do those of the nucellus whose cells form embryos vegetatively and entirely independent of gametophytic activities in a number of forms (*e. g.*, Funkia, Cœlebogyne, Citrus, Opuntia, *Alchemilla pastoralis*, etc.). This type of apogamy from a gametophyte which retains the sporophyte number of chromosomes may be found to hold a very close relation to apospory for there is the same reduction or omission of the processes of sporogenesis as is found in that phenomenon. However, since we know nothing of the cytological events of apospory it is unwise at present to follow the speculation further.

The peculiarities of parthenogenesis in the spermatophytes do not seem so remarkable since the discoveries recorded above. It is not strange that an egg should form an embryo without fertilization when its nucleus contains the sporophyte number of chromosomes. The most remarkable feature in this suppression of reduction phenomena in Antennaria, Thalictrum, and Alchemilla is the possibility of developing an embryo-sac with nuclei in the number and arrangement typical of the female gametophyte and yet with the sporophyte count of chromosomes. The embryo-sacs with their contents have clearly the morphology of female gametophytes and must be so considered in spite of the fact that their nuclei contain twice as many chromosomes as usual. It is clear that the potentialities of sporophyte and gametophyte involve other factors besides those of the chromosome count. This is a very important conclusion because we have been accustomed to lay great weight on the number of chromosomes as the cause of sporophytic and gametophytic developments respectively. We must recognize the presence of other factors determining alternation of generations besides the chromosomes.

There are two types of parthenogenesis in plants: (1) that in the thallophytes where there is no sporophytic generation, and (2) that in higher forms when the life history is complicated by an alternation of generation. We know nothing of the cytological conditions in the first group including such types as *Chara crinita*, Cutlaria, some species of Spirogyra and Zygnema and numbers of the lower Chlorophyceæ and Phæophyceæ whose motile gametes will germinate like zoöspores should they fail to conjugate with one another. But since there is no reason to suppose that there are reduction phenomena at gametogenesis, the unfertilized gamete is fully prepared with respect to the number of chromosomes to continue the parent stock. Dictyota must be excluded from this list since the parthenogenetic developments here are abortive. In the second group parthenogenesis is likely to prove to be the result of a suppression of reduction processes during sporogenesis by which a gametophyte generation retains the sporophyte number of chromosomes and in consequence is prepared to dispense with sexual processes in the development of a new sporophyte. Parthenogenetic development in animals seems to be similar in its essential cytological features to parthenogenesis and apogamy in plants. There may be a suppression of reduction processes somewhat comparable to that discussed above, which takes place, however, at the time of gametogenesis, whereby the egg nucleus retains the number of chromosomes characteristic of the parent. Or, through a fusion with the nucleus of the second polar body the egg nucleus is brought back to the normal condition with respect to the number of chromosomes of the parent stock. We cannot, however, consider in detail the forms of parthenogenesis in animals. They have been recently treated by Blackman (:04b) in comparison with conditions in plants.

Apogamous developments which involve wholly or in part other elements than gamete cells and nuclei are likely to be established in a number of groups of the thallophytes. The author has long believed that the cystocarps of some of the Rhodophyceæ develop apogamously, basing his conclusions on certain general peculiarities of the group and more particularly on a study of Ptilota (Davis, '96). Three species of this genus

were investigated and no developments from the carpogonia were found, but the cystocarp in all cases arose from a cell near the base of the group of procarps. These conditions together with the rarity of male plants on the American coasts (none have ever been reported) give strong evidence for apogamy in Ptilota. There are a number of genera of the Rhodophyceæ where similar conditions seem to obtain and which lead one to suspect that apogamy may not be very exceptional. However, the subject has been very little studied.

As is well known, the Ascomycetes furnish numbers of illustrations where ascogonia have not been found or appear in what seem to be reduced conditions and even when accompanied by so called antheridial filaments these latter have not been established as functional. De Bary recognized the possibility of apogamy in the development of the ascocarps of these forms and very little critical study has been given to them since his time. The trend of investigations in this group has been towards the more interesting problems of the establishment of sexuality in a few well known forms (*e. g.*, Gymnoascus, Sphærotheca, Pyronema, Monoascus, and among the lichens and Laboulbeniaceæ.)

It is generally believed that no sexual organs are present in the higher Basidiomycetes (Autobasidiomycetes). But the recent studies of Blackman (:04a) in the Uredinales, taken in relation to the well known nuclear fusions in the basidium, preceded by a mycelium containing paired (conjugate) nuclei, make it seem very probable that former sexual processes in the Basidiomycetes have been replaced by a remarkable type of apogamous development of a sporophyte generation. Blackman has traced the origin of the paired nuclei in the Uredinales (Phragmidium) to a structure preceding the æcidium, a structure which seems to be the remains of a female sexual organ. We will take up this investigation presently. There is then much reason for believing that a sporophyte generation in the Basidiomycetes arises apogamously in the creation of the paired nuclei and terminates with their fusion within the teleutospore or basidium.

The leptosporangiate ferns have furnished some of the best

illustrations of apogamy. Since Farlow's discovery in 1874 of an asexual sporophytic growth from the prothallus of *Pteris cretica* the list of apogamous pteridophytes has steadily increased until now the phenomenon is known in perhaps 25 forms. Farlow's investigation was followed by an extended study of De Bary ('78) on a large number of forms in the Polypodiaceæ and resulted in the establishment of similar sporophytic outgrowths in *Aspidium falcatum* and *Aspidium filix-mas cristatum*. De Bary proposed the term *apogamy* ('78, p. 479) for the general phenomenon and distinguished two forms, *apandry* the suppression of the male sexual organs which results in a parthenogenetic development of the egg, and *apogyny* for the suppression of the female. Sadebeck in the following year reported apogamy in Todea one of the Osmundaceæ (Schenk's *Handbuch der Botanik*, vol. 1, p. 231, 1879) thus extending the phenomenon to another family. And later apogamy was found in *Trichomanes alatum* one of the Hymenophyllaceæ (Bower, '88) and in *Selaginella rupestris* (Lyon, :04, p. 287).

The most important recent contribution on apogamy in ferns is by Lang ('98, abstract in *Annals of Bot.*, vol. 12, p. 251). This paper presents an able discussion of the phenomenon in its relation to alternation of generations and adds the very interesting discovery of sporangia borne directly on prothalli that were grown from spores. These sporangia were found in clusters on a thickened lobe or process from the prothalli of *Scolopendrium vulgare ramulosissimum* and *Nephrodium dilatum cristatum gracile*. The sporangia were perfectly normal in structure and they matured spores. It is probable that the process is itself sporophytic in character, *i. e.*, made up of cells with double the number of chromosomes of the true gametophytic portion of the prothallus, but cytological details are not known. Lang's study of the apogamous development of sporophytic buds on several forms of the Polypodiaceæ is the most detailed work on apogamy in the pteridophytes yet published. The apogamous growths appeared as the result of cultures which were watered entirely from below and exposed to direct sunlight, important departures from normal conditions surrounding fern prothalli. In all cases the prothalli developed normal

embryos when the conditions permitted of fertilization. We shall refer to some general considerations of Lang in our summary and conclusions on apogamy.

The spermatophytes present some exceedingly interesting examples of apogamous developments of embryos from nuclei within the embryo-sac other than the egg, as from antipodals (*Allium odorum*, Tretjakow, '95 ; Hegelmaier, '97) or synergids (*Alchemilla sericata*, Murbeck, : 02) or nuclei in the endosperm (Belanophora, Treub, '98 ; Lotsy, '99) but in these cases the sporophyte number of chromosomes is apparently present through a suppression of the reduction phenomenon of sporogenesis in the development of the embryo-sac.

We will now consider two studies which describe nuclear fusions preliminary to the appearance of apogamy (Blackman, : 04a ; Farmer, Moore, and Digby, : 03).

Blackman's (: 04a) observations on Phragmidium have cleared up to a great degree our understanding of the life history of the Uredinales. The chains of æcidiospores have been found to arise serially from "fertile cells" which form a group at the spot where an æcidium is to be developed. Each fertile cell has above it a sterile cell which, however, breaks down. The sterile and the "fertile cell" together may represent a female sexual organ, the sterile cell perhaps standing for the remains of a receptive structure similar to a trichogyne. The spermogonium consists of a large mass of antheridial filaments that abjoint sperms which are no longer functional. It is of course uncertain whether the "fertile cells" are morphologically the original female gametes since they may readily be other cells drawn into the process of apogamy. The "fertile cell" is stimulated to activity by the entrance of a second nucleus either from an adjacent hypha or from the cell below. The second nucleus does not fuse with the original nucleus in the "fertile cell" but the two come to lie close together as a paired or conjugate nucleus. The two nuclei of the pair divide simultaneously (conjugate mitosis) throughout a long series of nuclear divisions, beginning with the formation of æcidiospores and through the vegetative history which follows up to the production of the teleutospores where the members of the last pairs unite to form

the single fusion nuclei within these reproductive cells. There is much evidence that the period in the life history characterized by the presence of paired nuclei represents a sporophyte phase.

Blackman (:04a, p. 353) regards the process by which the second nucleus enters the "fertile cell," resulting in the conjugate nuclei, as a reduced form of ordinary fertilization. I have already pointed out in Section IV, "Asexual Cell Unions and Nuclear Fusions," what seem to me to be serious objections to the use of the term fertilization when it is clear that the second nucleus in the pair is morphologically not a gamete nucleus, and the subject was also taken up in the account of fertilization in the present section. Whatever may be the physiological interpretation of this remarkable phenomenon it seems to me clearly a substitute process for a former sexual condition and involves other elements than the original gametes and as such is a typical illustration of apogamy.

It seems probable that further studies in the Basidiomycetes will determine a similar origin for the paired nuclei preceding the basidium to that of Phragmidium but without any trace of former sexual organs at least in the higher groups. And these conditions must signify the complete disappearance of structures representing sexual organs and the substitution of an apogamous development of the sporophyte generation for the sexual act. In this connection the interesting nuclear fusions in the ascus are of great interest for they may hold relations to degenerate sexual conditions in the Ascomycetes.

Farmer, Moore, and Digby (:03) have reported some remarkable nuclear fusions preceding the apogamous development of the sporophytes of Nephrodium, which have many points of resemblance to the apogamous phenomena in the Uredinales just described. These authors find that cells of the prothallus from which the sporophytic outgrowths arise, become binucleate through the migration of nuclei from neighboring cells. The two nuclei may remain separate for some time or they may fuse at once. They regard the whole process "as a kind of irregular fertilization" by which the outgrowth destined to form the sporophyte becomes supplied with nuclei containing the double number of chromosomes. It seems to me unfortunate to asso-

ciate the term fertilization with this phenomenon, whatever may be the physiological significance of the nuclear fusions, because we are not dealing with gametes and there cannot be involved in the process anything of the long phylogenetic history of sexual differentiation in the group. We considered these matters in some detail in that portion of this section entitled "Fertilization."

With respect to the factors which determine apogamy it must be confessed that we are still in the dark. Lang's ('98) studies on fern prothalli, however, throw some light on the problem. In some twenty forms of the Polypodiaceæ apogamy resulted when the prothalli were kept from direct contact with the water (*i. e.*, were watered from below) and exposed to direct sunlight. When watered from above these same forms developed normal embryos from eggs. It is clear that the suppression of conditions which make fertilization possible (*i. e.*, water over the surface of the prothallus), possibly aided by sunlight which may cause irregularities of growth, induced the development of cylindrical processes from which the apogamous sporophytes arose and which bore sporangia in two forms. It seems hard to draw more precise conclusions from these experiments other than that the normal life history is checked at a critical period (fertilization) and the plant is forced into expressions of vegetative activity. The conclusions of Farmer, Moore, and Digby (:03) offer an explanation of how the developments may take on sporophytic characters through the fusion of nuclei in the tissues and the establishment of a sporophyte number of chromosomes.

Strasburger suggests that apogamy in Alchemilla may be the result of a weakening of sexual power associated with excessive mutative tendencies. This would seem to imply that exceptional vegetative activity, with the appearance of much variation under favoring conditions, may be combined with apogamy. It is of course a well known fact that a high degree of cultivation tends to lessen the fertility of a form unless guarded by careful selection. A weakened sexual fertility due to excessive vegetative activity is likely to be replaced by forms of vegetative reproduction. When the process of sporogenesis becomes so

reduced or modified that the female gametophyte retains the sporophyte number of chromosomes as in the embryo-sac of Alchemilla and Thalictrum the apogamous development of embryos is to be expected.

The discovery of apospory in such variable and perhaps mutating genera as Alchemilla, Taraxacum, and Hieracium suggests quite a new line of research with possibilities of a clearer understanding of the origin of mutations. It is very interesting that these widespread and successful genera should give evidence of such strong apogamous habits for it seems to indicate an evolutionary tendency in the higher plants of great significance. These forms with Thalictrum are representatives of three large, divergent and very successful orders (Ranales, Rosales, and Compositales) and it suggests the probability that apogamy will be found to be widespread in the spermatophytes. Its bearing on the establishment of extreme variations and mutations may be of the utmost significance for it is clear that the suppression of sexuality would remove sports and mutants at once from the swamping effects of cross-fertilization. The sudden appearance of mutants in some groups and their ability to hold true may indeed be found to rest on the establishment of apogamy in the form. This is at least a possibility which must be considered in cytological investigations on mutants and has not yet received attention.

The subject of apogamy touches another topic of importance, namely, the theory of *homologous* generations as contrasted with *antithetic* generations in comparisons of sporophyte with gametophyte. We shall not take up this discussion in detail here. It must have been apparent to the reader that the present treatment of the critical periods in the life history of plants is based on the conviction of the correctness of the latter view which has had the support of Celakovsky, Strasburger, Bower, Vaisey, and Klebs. The theory of *homologous* generations as held by Pringsheim and Scott is admirably discussed by Lang ('98) in connection with his studies on apogamy and also in a briefer note (*Annals of Bot.*, vol. 12, p. 583). Lang seemed inclined to the opinion that the facts of apogamy and apospory in ferns lent support to the theory of homologous generations since the

prothallus can so readily take on sporophytic potentialities and the sporophyte develop gametophytes vegetatively. But Lang recognized that the importance of this evidence would be minimized should it be found to depend on changes of nuclear structure. These nuclear changes have been established at least for apogamy, either in the suppression of the reduction phenomena of sporogenesis or by the substitution of asexual nuclear fusions for the sexual act, and the argument for antithetic alternation of generations seems to the writer stronger to-day than ever before.

6. Apospory.

Apospory is the suppression of all processes of sporogenesis and the development of a gametophyte generation directly from the sporophyte. The term was first proposed by Vines (*Jour. of Bot.*, 1878, p. 355) in a discussion of the life history of Chara and adopted by Bower ('86, '87) in a general treatment of the subject based on Druery's ('86a, '86b) discoveries of prothalli developed in place of sporangia directly upon the leaves of *Athyrium filix-fœmina* and its variety *clarissima*. The phenomenon of apospory is best known among the ferns where it has been most extensively studied but so far no cytological investigations have been published. Since apospory results in the development of a gametophyte generation (presumably with the gametophyte number of chromosomes) without the preliminary process of sporogenesis it becomes a very interesting problem to know just how this reduction of the chromosomes is effected.

Apospory is probably not uncommon in the mosses and has also been reported for the liverwort Anthoceros. The independent studies of Pringsheim ('76) and Stahl ('76) established the facts that pieces of the sporophyte stalk (seta) of Hypnum, Amblystegium, Bryum, and Ceratodon when placed on damp soil developed a protonema which in its turn produced leafy moss gametophytes. Stahl also found in Ceratodon that protonemata may arise from the capsule wall and Brizi ('92) discovered a similar development from the atrophied capsule of *Funaria hygrometrica*. Correns ('99a, p. 421) has confirmed the conclu-

sions of Pringsheim and Stahl in species of Funaria, Hypnum, and Amblystegium and obtained negative results in a number of other forms, and presents an excellent review of the subject. Lang (:01) discovered that small pieces of the sporophyte of *Anthoceros lævis* when laid on damp sand produced green outgrowths which took on the structure of young gametophytes and developed rhizoids. These aposporous gametophytes most commonly arose from subepidermal cells, but they may come from any layer of the cortex down to the archesporial cylinder. It seems probable that the mosses at least among the bryophytes are able to reproduce themselves apogamously without difficulty, when normal processes of sporogenesis are interfered with and if the sporophytic tissue is in contact with moisture.

The leptosporangiate ferns, however, furnish the most conspicuous illustrations of apospory as they do of apogamy. Indeed, the two phenomena are known to occur in the same form in a number of instances (*e. g.*, *Athyrium filix-fœmina*, *Nephrodium filix-mas*, *Scolopendrium vulgare*, *Trichomanes alatum*, etc.). Beginning with the discovery by Druery ('86a, '86b) of apospory in *Athyrium filix-fœmina* and its variety *clarissima* the list has steadily grown until now apospory is recorded for about ten forms. In Druery's forms the prothalli developed from arrested sporangia and the spore alone is left out of the life cycle. But Bower ('86) very shortly brought forward in *Polystichum angulare pulcherrimum* a form in which prothalli are developed as simple vegetative outgrowths from the tips of the leaves and the life history is thus shortened by the omission of both spores and sporangia. This condition is exactly analogous to the development of protonemata from vegetative cells of the sporophytes of mosses and Anthoceros. The following year Bower ('87) presented a very full account of the forms of Athyrium and Polystichum just described, and a general discussion of the phenomenon of apospory. Bower ('88) then extended the illustrations of apospory to two species of Trichomanes, of the Hymenophyllaceæ; Farlow ('89) reported it for *Pteris aquilina*, and Druery ('93) in *Lastrea pseudo-mas cristata* and ('95) for *Scolopendrium vulgare crispum*. The exceptional amount of fern variation both in nature and under cultivation has not been

generally appreciated and the studies on apospory and apogamy indicate that much of it is associated with these fundamental modifications of the life history (Druery, :01).

As to the cause of apospory we are as much in the dark as in the case of apogamy. The phenomenon is clearly associated in some forms with disturbances in the normal vegetative life of the sporophytes. This is particularly true in the cases of mosses and Anthoceros and has been suggested for the ferns. Thus aposporous developments in *Pteris aquilina* are from leaves which are generally smaller than the normal and whose margins are curled so that the leaf often appears somewhat withered and is easily recognized at a distance. Bower ('87, p. 322) is inclined to regard the phenomenon in the ferns as a sport and does not consider that it has deep morphological significance or that it offers serious difficulty to the acceptance of the theory of an antithetic alternation of generations.

As we have stated there have been no cytological studies upon apospory but there seem to be two possible explanations. That which is likely to suggest itself first calls for reduction phenomena at the time of the aposporous development by which the nuclei of the sporophytic tissues may come to contain the gametophyte number of chromosomes and are therefore capable of developing the sexual generation. But there is another possibility which has not yet been considered. We know for several of the spermatophytes (Antennaria, Juel, :00; Thalictrum, Overton, :04; Alchemilla, Strasburger, :04c) that the processes of sporogenesis may be suppressed and yet a structure be developed with the morphology of the gametophyte generation. Thus the embryo-sac will contain the usual number of nuclei grouped in the typical manner but these nuclei still have the sporophyte count of chromosomes. It seems probable then that the development of a gametophyte may result through an interference with the normal life history and under conditions favorable to the gametophyte even though the nuclei retain the sporophyte number of chromosomes. And it is possible that some of the aposporous developments in bryophytes and pteridophytes may be of this character. It is quite futile at present to carry this speculation further. What is desired is some cytological facts.

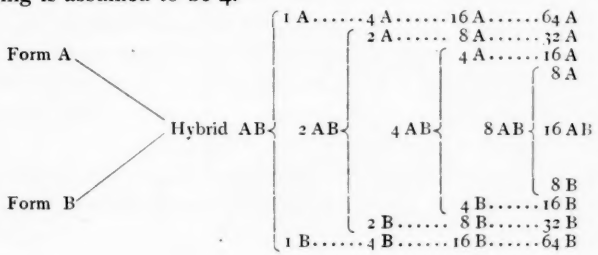
7. HYBRIDIZATION.

This is not to be a detailed discussion of the facts and theories of hybridization, a subject far too extensive for the purposes of our treatment. We shall only consider some of the bearings of the recent studies on fertilization and reduction phenomena upon the problems of hybridization treating it as a critical phase in the life history of the organisms concerned. Until recently the attempts to formulate definite laws for the formation of hybrids and their progeny upon a physical basis have not been satisfactory. But the work of a number of breeders all of whom owe their results in large part to a quick appreciation of Mendel's epoch-making contributions have brought much order out of what was a very confused subject. And accompanying the work of this group must be added the equally important conclusions of a number of cytologists whose investigations on the structure and behavior of nuclei in the critical periods of fertilization and chromosome reduction have done much to place Mendelian principles upon a cytological basis. We shall deal with the work of the latter group, for their contributions concern intimately the subject matter of these papers.

We shall not review the conclusions of Mendel except to point out the relations of some of his principles to cytological phenomena. The two papers of Mendel appeared in the proceedings of a natural history society of Brünn, Austria, under the dates 1865 and 1869. They lay buried until 1900 when De Vries, Correns, and Tschermak independently rediscovered them and called the attention of the scientific world to their worth. Soon after, Bateson published a translation of the two papers (*Mendel's Principles of Heredity*, Cambridge, 1902) with an introduction and a defense against the criticisms of Professor Wheldon. There have naturally been many reviews and short discussions of Mendelian theories and among them that of Castle entitled "Mendel's Laws of Heredity" (*Science*, vol. 18, p. 396, 1903) and Professor Bailey's "Lecture IV" in *Plant Breeding*, 1904, will perhaps give the reader the clearest and most concise statements.

The most striking feature of Mendel's investigations and those

of others, who have confirmed his conclusions, is the discovery in a number of animals and plants that the germ cells of the hybrid may be pure with respect to certain characters of the parents which are crossed. This principle is not without exceptions where the conditions are apparently complicated by unusual factors but the phenomenon when present is so striking as to command immediate attention and call for an explanation on a cytological basis. The purity of the germ cells of hybrids means in the words of Castle that "the hybrid, whatever its own character, produces ripe germ cells which bear only the pure characters of one parent or the other." Thus if two forms A and B are crossed the hybrid will have embodied in itself the characters AB, one of which however may lie latent, *i. e.*, may not be visible in the hybrid. Such a latent character when present is termed recessive while the prominent character is termed dominant. In a simple case some of the offspring of the hybrid AB will be found to have the character of A alone, some of them of B alone, and some of them will again have the mixed characters AB. If experiments are carried out on an extensive scale the proportions of these offspring from the hybrid may exhibit the remarkable fact that there are about twice as many forms of AB as either A or B, *i. e.*, the proportions of A's, AB's, and B's are in the ratio of 1 : 2 : 1. Furthermore the offspring of A when bred among themselves remain absolutely true producing a succession of pure forms all A's and the same results follow when the offspring of B are closely bred. But when forms with the mixed characters AB are bred with one another their offspring break up as before into three types A, AB, and B in numerical proportions expressed by the same ratio 1 : 2 : 1. The history is simply told in the following diagram where the number of offspring is assumed to be 4.



This remarkable proportion of forms derived from the hybrids AB, *i. e.*, A, AB, and B in the ratio 1 : 2 : 1 can only be explained on the assumption that the germ cells of the hybrid are pure with respect to the characters of either one or the other of the parents. The gametes from the hybrid, with the pure characters of either A or B and approximately equal in number, may unite with one another in three possible combinations AA, AB, or BB forming three types of offspring, one pure A, another mixed AB, and the last pure B. By the law of chance the proportions of these combinations (AA, AB, and BB) in a simple case will be in the ratio 1 : 2 : 1. This assumption of the purity of the germ cells of hybrids has been found to conform with the facts in a number of simple experiments where two characters such as A and B were sharply contrasted. When one of the characters in the hybrid is dominant and the other recessive the ratio can be expressed as D : DR : R as 1 : 2 : 1 which is merely a substitution of D and R for the characters A and B.

There are of course many factors which tend to modify the ratios as stated above and complicate the results. Thus the normal number of gametes may be of varying vigor and mortality so that there will be proportionately more or less of one type of fusion than is called for by the law of chance. Sometimes the characters of the parents remain evenly balanced in the hybrid and refuse to split up in the succeeding generations, remaining in a stable union in the germ cells produced by the hybrid. Such conditions prove exceptions both to the law of dominance and to that of purity of the germ cells. From these exceptions and particularly the last it is difficult to believe that any large proportion of the germ cells is *absolutely* pure, *i. e.*, bearing only the pure characters of one parent or the other. However, there is much evidence from our knowledge of the distribution of the chromosomes from one generation to the next, that certain relations are possible in the separation of germ plasm which approximate the ratios of Mendel's law and while rarely giving *absolutely* pure germ cells nevertheless do make possible a large proportion of *relatively* pure cells.

Let us examine now the chromosome history as a possible physical basis for the Mendelian principles. Such considerations

must rest on the assumption of what is termed the individuality of the chromosome. This means that the chromosome is believed to be a permanent organ of the cell which never loses its organic entity although the form may be frequently obscured, as in the resting nucleus, and which reproduces by fission during mitosis. We have given in other connections the evidence upon which the above view rests, evidence accumulated from the studies of the critical periods of gametogenesis, fertilization, and sporogenesis (with its reduction phenomena) in plants and of gametogenesis and fertilization in animals. All investigations indicate that paternal and maternal chromosomes maintain complete independence in the sexually formed cell or fertilized egg and in the mitoses of cleavage so far as these have been followed. Also, descendants of the chromosomes which became associated with fertilization have been recognized by their form at the end of the life history during the reduction phenomena of gametogenesis in certain animals (Sutton, :02, :03; Montgomery, :04) and of sporogenesis in the hybrids of Drosera (Rosenberg, :04a, :04b). Furthermore, the entire history of chromosome reduction in both animals and plants finds a satisfactory explanation only in the belief that descendants of maternal and paternal chromosomes are distributed as organic entities by the peculiar mitoses of this period.

There is a general agreement that the somatic chromosomes of animals and the sporophytic of plants become grouped in pairs to form bivalent structures before the heterotypic mitosis of the reduction division whether this be present in the primary gametocyte (animals) or the spore mother-cell (plants). The bivalent chromosomes (pairs of chromosomes, dyads) may become transformed into tetrads before the heterotypic mitosis by a division of each chromosome in the pair, as is characteristic of animals, or this division may be delayed until a somewhat later period during the heterotypic mitosis, as in plants. We are not concerned now with the dispute as to how the pairs of chromosomes come to lie side by side to form the bivalent structure or how tetrads are developed, activities which may indeed be various in different types and which will only be understood by a greater body of observations than we have at present (see dis-

cussion of "Reduction of Chromosomes"). The important point for us is the belief that the appearance of the bivalent chromosomes during reduction is due to the temporary union of somatic or sporophytic chromosomes in pairs and further that the reducing divisions distribute the members of the pair, which are believed to be descendants of the maternal and paternal chromosomes of the previous generation, as organic entities to the generation which is to follow.

It is difficult to overestimate the importance of this generalization. If the program prove to be correct as stated above and if the chromosome is established beyond doubt as a self-perpetuating organ of the cell and a bearer of hereditary characters we have then the possibility of studying the actual manner in which these structures are passed on from one generation to the next and perhaps determine the ratios or combinations through which the distribution is effected. The difficulty of making an exact determination of ratios in any form so far studied lies in our inability to distinguish the chromosomes of maternal and paternal origin. There is much evidence that the pairs of somatic and sporophytic elements, which form the bivalent chromosomes of the reduction mitoses of animals and plants respectively, are of different parentage but we do not know whether or not there is any rule in the arrangement of the pairs on the spindles of these mitoses although this is hardly to be expected. Cannon (:02, :03a) and others have held that the mitoses of reduction brought about the complete separation of the maternal and paternal chromosomes so that two of the resultant four nuclei contain chromosomes from one parent and two from the other, and the germ cells are in consequence *absolutely* pure in character. But this view was soon shown by Sutton (:03, p. 233; accepted by Cannon, :03b) to be at variance with the facts of breeding for if germ cells of hybrids are *absolutely* pure there could be no further change by cross-breeding and the first cross would be repeated over and over again without any divergence from the type, which is contrary to experience and fact. The pairs of chromosomes are probably arranged in every possible order and the maternal and paternal elements are distributed in every possible combination by the reducing

divisions. If this is true then by the law of chance the proportions of germ cells of the hybrid which are *absolutely* pure (containing chromosomes entirely from one parent) would be small. Likewise there would be a small proportion of germ cells in which the paternal and maternal chromosomes are equally distributed. And in contrast to these two groups the great majority of germ cells would have a marked preponderance of chromosomes derived from one parent or the other and this condition may be termed one of *relative* purity.

We shall now summarize the cytological evidence for the conclusions of the paragraph above, first with respect to the actual distribution of the somatic and sporophytic chromosomes as entities during the mitoses of reduction, and second as to the probability of the bivalent chromosomes consisting of a pair of maternal and paternal elements. The evidence on the first point has been treated as regards plants in our own account of "Reduction of the Chromosomes" and need not be repeated. With respect to the possibilities of distinguishing maternal and paternal chromosomes throughout a life history and especially at the period of chromosome reduction we must consider briefly the remarkably favorable studies of Sutton, Montgomery, Moenkhaus, Baumgartner, and Rosenberg.

Sutton (:02, :03) discovered in the "lubber grasshopper" (*Brachystola magna*) a form in which the somatic chromosomes, 23 in number, are markedly different in size, presenting a graded series with respect to pairs in which the two elements are approximately equal. There are then 11 types of chromosomes in two groups, a pair of each type, and in addition an accessory chromosome which remains apart from the rest in a special vesicle of its own. These two sets of 11 chromosomes appear with regularity throughout the mitoses leading up to the reduction divisions of spermatogenesis. Previous to the reducing divisions the chromosomes of each pair become closely associated end to end so that 11 threads appear which form 11 bivalent chromosomes (dyads) that later become tetrads through the division of each chromosome in the pair. Sutton concludes that the somatic chromosomes which make up each bivalent structure conjugate during synapsis and that the transverse fission which

appears during the formation of the tetrad simply separates the two somatic chromosomes of the pair, while the longitudinal fission is the usual division of chromosomes, appearing prematurely at this time. The conclusion is natural that the two series of the 11 pairs consist of maternal and paternal chromosomes which are distributed as organic entities by the reducing divisions. But there are no reasons for supposing that all of the paternal chromosomes will pass into one set of germ cells and all of the maternal into another but rather that the ratios of distribution will be by the law of chance according to which the great majority of germ cells will have a marked preponderance of chromosomes from one parent or the other, and will therefore be *relatively* pure. An exceedingly small proportion of germ cells may, by the law of chance, contain chromosomes entirely of maternal or paternal extraction, and an equally small proportion may contain 6 chromosomes of one parent and 5 of the other. The accessory chromosome divides but once during the mitoses of spermatogenesis so that two of the spermatozoids have 11 chromosomes and two 12. No accessory chromosome appears in the mitoses of oögenesis indicating that the female insect lacks this structure which confirms the belief of McClung (:02) and others that the accessory chromosome is a determinant of the male sex.

Montgomery in a series of studies upon insects and Amphibians, which are summarized in a recent paper (:04), reached conclusions in striking support of the theories of the individuality of the chromosomes, the association of pairs of chromosomes during synapsis to form bivalent structures and the probability of the elements of each pair (bivalent chromosomes) being of maternal and paternal origin respectively. His results on the last point are of especial interest in relation to hybridization. In a large number of insects, chiefly Hemiptera, Montgomery has found pairs of chromosomes, which he terms heterochromosomes, much smaller or much larger than the others and these may be followed through mitosis from one nucleus to another. The heterochromosomes of each pair are known to unite with one another during synapsis to form the bivalent chromosomes of the reduction mitoses and they then become separated, each

dividing once, so that every germ cell receives a single heterochromosome of whatever sort. Fertilization then brings the heterochromosomes together again in pairs until the next period of chromosome reduction. This history is then parallel to Sutton's account of the lubber grasshopper (Brachystola), the difference being that the latter form presents a remarkably graded set of paired chromosomes. Montgomery regards the small chromosomes and the accessory chromosome as structures tending to disappear in a process of evolution from a higher chromosomal number to a lower.

Moenkhaus (:04) crossed reciprocally two species of fishes (*Fundulus heteroclitus* and *Menidia notata*) and obtained hybrid embryos which reached an advanced stage of development. The chromosomes of the parents are readily distinguished by size and form. These chromosomes were followed throughout the development of the hybrid embryo and were found to retain their peculiarities so that the two sets may be easily separated in favorable tissues. This investigation furnishes some of the strongest evidence of the individuality of the chromosome and the complete independence throughout the life history of the two sets derived from each parent. Could these hybrid embryos be raised to maturity we should expect to find during spermatogenesis and oögenesis an association of the chromosomes in pairs, those of paternal extraction with those of maternal to form the bivalent chromosomes preliminary to the reducing divisions, and a distribution to the sexual cells in varying proportions which would, however, give a very large ratio of *relatively* pure germ cells.

Baumgartner (:04) in studies upon spermatogenesis in the cricket (Gryllus) was able to distinguish the chromosomes by their form, following them through the mitoses of reduction. Most of the chromosomes have the form of straight or bent rods but there are apparently two rings in each set in *G. domesticus*. The variation in the form of chromosomes in the nucleus is well known but it has not been supposed that a definite form might be characteristic of an element and be maintained throughout the successive mitoses of a life history as seems probable from Baumgartner's results.

Rosenberg's (:04a, :04b) studies on hybrids of *Drosera rotundifolia* (with ten chromosomes in the gametophyte) and *D. longifolia* (with twenty chromosomes) offer clear evidence that the chromosomes which unite in pairs to form bivalent structures preliminary to the reduction phenomena of sporogenesis are of different parentage. The sporophyte number of chromosomes in the hybrid is thirty, as would be expected. The reduced number appearing at the first mitosis of sporogenesis is, however, not fifteen but twenty chromosomes, ten of which are plainly double the size of the other ten. The explanation of this interesting condition is that the ten chromosomes of *D. rotundifolia* unite with one half of the twenty chromosomes of *D. longifolia* giving ten large bivalent structures accompanied by the ten chromosomes of *D. longifolia* which are without mates. This explanation finds clear support in the facts that the chromosomes of *D. rotundifolia* are larger than those of *D. longifolia* and that the bivalent structure consists of a larger and a smaller element thus giving clear evidence that the pairs of chromosomes which unite in Drosera are of different parentage. The single chromosomes which are without mates may pass to one or the other of the poles of the spindle or may be left behind when the daughter nuclei are formed.

This group of investigations illustrates very clearly the character of the evidence that is leading many biologists to assign to the chromosomes the functions of bearing and distributing hereditary characters. The question at once comes up as to whether or not the chromosomes may differ among themselves to a greater or less extent even in the same species or individual. Montgomery, Sutton, with others, have established a difference in the *size* of chromosomes. Baumgartner distinguishes differences in *form* in the same species and the studies of Moenkhaus and Rosenberg have shown that the chromosomes of different parents may retain their peculiarities of *form* in hybrids and be really separated. To these investigations should be added the recent conclusions of Boveri (:02, :04), that chromosomes actually differ in *function*. Boveri found that the chromosomes of eggs of echinoderms that were fertilized by two or more sperms are distributed by multipolar spindles to a varying number of

blastomeres which in consequence received a varying number and assortment of chromosomes. Boveri then separated these blastomeres and followed their independent development into larval stages which exhibited marked differences in form that could be correlated with the irregularities in the number of chromosomes contained in each, thus suggesting that specific chromosomes have specific functions. With this sort of evidence accumulating from both the morphological and physiological side it is not surprising that many biologists believe that specific characters are actually held or are controlled by chromosomes or groups of chromosomes.

Such views of course presuppose that the chromosomes retain a high degree of independence of one another and that variation is expressed chiefly through different combinations of chromosomes and not by modifications of the chromosomes themselves. Yet there is strong evidence of an actual mixing or interchange of the idioplasm among the chromosomes. This possibility which is of course contradictory to the view of the *complete* independence of the chromosomes finds its chief support in the close association of the pairs of chromosomes with the organization of the reduced number of bivalent structures during synapsis. These pairs have been reported so intimately united as to be actually fused. Allen (:05) has described for Lilium the union of two sets of chromomeres, one believed to be derived from a paternal spirem and the other from a maternal, which come to lie side by side during synapsis and unite to form a spirem with a single series of fusion chromomeres. This single (fusion) spirem later splits longitudinally and the two halves are regarded as again representing maternal and paternal spirems but there are evidently opportunities during the period of fusion for significant reciprocal interaction between the two idioplasms. This conception of the fusion of idioplasm from the two parents is an old view which has been held by such well known biologists as Hertwig and Strasburger.

De Vries (:03) has recently discussed the significance of the pairing of chromosomes before the heterotypic mitosis in relation to the theory of pangenesis. He conceives the paternal and maternal chromosomes as coming together during synapsis in

homologous pairs so that corresponding pangenes or groups of pangenes are brought together and that there may be a mutual interchange or transfer of idioplasm with the result that the chromosomes after separating may contain a mixed set of pangenes although each is supposed to have a complete assortment. The interchange makes possible all forms of combinations of the pangenes in the two sets, according to the laws of chance, which might be expressed in proportions that would approximate in some cases the ratios of Mendel. If the parents are widely different from one another their idioplasm may not correspond sufficiently to make possible this union and interchange of pangenes so that the process is suppressed and the hybrid is sterile.

Allen (:05, p. 247) points out that the union of two spirems during synapsis with the fusion of two sets of chromomeres, according to his account of the lily, offers a number of possibilities with respect to the constitution of idioplasm following the reduction mitosis. (1) There may be such a fusion of elementary units that a single idioplasm is formed different from either parent which would of course be distributed equally to the reproductive cells by the subsequent double longitudinal fission of the single (fusion) spirem. This would be expected to give hybrids of much the same form in every instance and these would remain stable (constant). (2) There may be a greater or less mixing or modification of units but without the actual union and formation of a new idioplasm in the hybrid. Then by the splitting of the single (fusion) spirem there might result a distribution of the mixed idioplasm following ratios or proportions approximating Mendel's law. (3) There may be in part a fusion and in part a mixing of idioplasm which would be expected to result in a varied combination of parental characters in the offspring. (4) While the chromosomes may be distributed according to ratios similar to Mendel's principles their respective characters may be greatly modified by their temporary union during synapsis. (5) Portions of the idioplasm may interact upon one another so that when they are separated by the reduction mitoses their character has become variously modified. (6) Finally, Allen, of course, recognizes the possibility that parental

idioplasm may be separated so purely by the longitudinal splitting of the single (fusion) spirem or through the distribution of unmodified sporophytic or somatic chromosomes as to give *absolutely* and *relatively* pure germ cells through Mendelian laws.

Allen's discussion, very briefly summarized above, is important for the emphasis which is laid upon the significance of a possible mixing of the parental idioplasms in the more or less complete union of chromatic material, which is generally recognized as characteristic of synapsis. There is a general tendency to rest content when the chromosomes are accounted for as units while they are merely the grosser form of expression of the idioplasm whose final architecture is intricate far beyond our present powers of analysis. Allen's own studies upon the events of synapsis in the lily with the regular fusion in pairs of chromomeres of different parentage may well cause one to hesitate in a full acceptance of the chromosome as fixed and unchanged in its organic constitution throughout the life history. The phenomenon of hybridization is far too complex to be explained in terms of simple ratios and while some characters may be paired or correlated in proportions that can be expressed by mathematical formulæ there is little probability that the assemblage of characters which make the species can be so definitely grouped as the strongest disciples of Mendel may hope. However, a great forward step has been taken and we may expect important results from the empirical methods so clearly defined by Mendel and by the close investigation that cytologists are making of the history of idioplasmic structures (chromosomes) during ontogeny.

8. Xenia.

Xenia is the "immediate or direct effect of pollen on the character of seeds and fruits." The term was first proposed by Focke, in 1881, and is now well established. Xenia has long been known to the plant breeder as one of the most interesting and puzzling problems of hybridization. The botanist has naturally looked for the results of hybridization in the development of the embryo from the seed since this structure has received

the substance of the sperm nucleus of the male parent. But facts have clearly shown that the pollen may also affect the structure of the endosperm in the seed as well as cause the development of the embryo. Since the endosperm holds no genetic relation to the embryo it has seemed very remarkable that it should take on hybrid qualities. It has also been claimed that other regions of the seed or fruit, such as portions of the pericarp were also affected, but it is doubtful whether this is really so or at least whether such changes are truly a feature of the protoplasmic structure and thus deeply seated in the organism as a feature of hybridization.

It is only within recent years that a satisfactory theory has been suggested for the influence of pollen outside of the embryo. And this explanation rests on the discovery of the activities of the second sperm nucleus which enters the embryo-sac and which is known in some cases to unite with the polar nuclei constituting a triple nuclear fusion within the sac that is generally known as "double fertilization." We have briefly referred to the phenomenon in the latter part of the account of "Asexual Cell Unions and Nuclear Fusions" in Section IV and shall take it up now in greater detail. The best account of xenia is a very clear treatment by Webber, in 1900.

The explanation of xenia upon the facts of "double fertilization" was proposed almost simultaneously by De Vries ('99, :00), Correns ('99b), and Webber (:00). Double fertilization was first observed by Nawaschin ('98) in Lilium and Fritillaria and shortly after was described in greater detail by Guignard ('99b) in other species of the same genera and in Endymion. Since these discoveries the phenomenon has been reported by a number of investigators in many other forms representing widely divergent groups in the Monocotyledonæ and Dicotyledonæ and there is every reason to believe that it is widespread in the angiosperms. A review of the recent literature is given by Coulter and Chamberlain (*Morphology of the Angiosperms*, 1903, p. 156). There is no fixed order in the events of the triple nuclear fusion of "double fertilization." The polar nuclei may have united at the time when the pollen tube enters the embryo-sac, in which case the second sperm nucleus coalesces with an organized fusion

endosperm nucleus. Or, the two polar nuclei and the sperm nucleus may all three fuse together practically simultaneously. And again the sperm nucleus may unite first with one of the polar nuclei and the second be drawn later into the triple fusion. But no cases seem to have been reported in which but one polar nucleus unites with the sperm leaving the other free although such a combination may be expected. Also, no one has observed an independent division of the sperm nucleus within the endosperm, although as we shall see, there are reasons for believing that such a development may sometimes take place.

We have already given in Section IV the reason why these triple nuclear fusions may be kept apart from sexual phenomena since we have no knowledge of the phylogenetic history of the processes involved. It seems best at least for the present to regard the phenomenon as a special development associated with the peculiar and highly specialized conditions within the embryo-sac. This detailed and highly difficult problem of phylogeny has no especial bearing on the physiological features of xenia with which we are at present concerned.

The best understood examples of xenia are found in the hybrids of maize and are clearly described in the very interesting paper of Webber (:00). As is well known, some of the varieties of corn are distinguished among other characters by the color of the kernels, which are blue, red, yellow, and white, and also by the surface, which is smooth in the starchy corns (flint or dent) and wrinkled in the sugary sweet corns. When well marked pure races are grown out of reach of chance cross-pollination, the offspring remain true to their seed characters but it has long been known that the varieties of corn hybridize very readily so that when grown close together the ears will very frequently present seeds mixed as to color and texture. Thus when exposed to cross-pollination a corn which is characteristically yellow or white may bear blue or red kernels or a form with wrinkled and starchy kernels may develop smooth starchy corn if varieties with these characters are in the vicinity. The color character is known to lie in these examples in the outer layer of the endosperm (aleurone layer) and of course the food material whether prevailingly starch or sugar, which gives the

surface a texture smooth or wrinkled, is stored within the endosperm.

The clearness of xenia in the maize has led to a number of careful studies on cross-pollination beginning with the work of Vilmorin (1866), Hildebrand (1867), and Friedrich Körnicke (1872). The possible explanation of xenia in maize through "double fertilization" which introduces qualities of the male parent from the pollen into the endosperm was suggested by experiments of De Vries on hybridizing maize in the summers of 1898–99 and Correns and Webber in 1899. De Vries ('99, :00) pollinated a wrinkled-seeded sugar corn from a variety of smooth starchy corn and obtained smooth starchy kernels which when cultivated in the succeeding summer were found to be true hybrids. He concluded that this furnished experimental proof that the endosperm of the sugar corn was affected by the entrance of a sperm nucleus from the starchy variety according to the theory of "double fertilization" proposed by Nawaschin ('98).

Correns ('99b) in the same year expressed similar conclusions in a clear statement of the theoretical aspects of the problem of xenia as found in *Zea mays*. Correns advanced a number of propositions some of which should be noted for their speculative interest. Thus he states (proposition 7) that the influence of the new pollen (*i. e.*, from the male parent of the hybrid) is expressed as xenia only in the endosperm and (proposition 8) only in the pigment present or the chemical nature of the reserve material whether starchy or sugary. If the two races differ only in the presence of one character, as in the color of the aleurone layer, that character is only found in xenia when brought by the pollen (proposition 10). Xenia is then only expressed in a hybrid (proposition 14) by the formation of a pigment which the race of the female parent does not possess or of a more complicated chemical compound (such as starch) in place of a simpler (as dextrin). Correns (:01) later presented in a lengthy paper, beautifully illustrated, the full results of his studies on xenia in maize with a discussion of the hybrids.

Webber (:00) also simultaneously with De Vries and Correns conducted extensive experiments in hybridizing a number of

varieties of corn distinguished by the color of the kernels, which were white, yellow, red, or blue and by the texture whether smooth, hard, and starchy (dent or flint corn) or wrinkled and sugary (sweet corn). The results of his investigation are admirably presented with excellent illustrations. He found that the smooth kernel and starchy endosperm of the dent and flint corn were transmitted very conspicuously as xenia when these forms were employed as the male in crossing with the sweet corns whose kernels are wrinkled and sugary. The characters of the sweet corns do not seem to be expressed as xenia when smooth, starchy, dent corn is used as the female member of the hybrid. This experiment would seem to support Correns' proposition number 14 that a more complicated compound is always formed in xenia in place of a less complex. But Webber found that flint corn, which is smooth and starchy, when pollinated with a form of sweet corn developed the wrinkled kernel and sugary type of endosperm of the male member indicating that this rule of Correns is not universal. And McClure ('92) obtained similar results in crossing a white dent race with pollen of Black Mexican which is a sugar corn with black kernels. The product in this case showed xenia clearly in having the wrinkled blue-black kernels of the male sugar corn.

Some of Webber's most striking results were obtained in pollinating yellow and white corns with blue-black and red races. The color was transmitted as xenia in a most striking manner. Webber agrees with other authors that the color is only present in the endosperm of the kernels. Thus the red of certain dent corn, which lies in the pericarp, is not passed on as xenia and McClure observed the same facts in experiments with cranberry corn whose color lies in the seed coat and is not transmitted when employed as the male member in crossing with white corns. Webber's experiments show, as do those of other investigators, that the absence of color in the kernels of the male parent does not seem to affect the tint of the kernels when the female is markedly colored, in agreement with Correns' proposition number 10. But Webber is not convinced that some influence might not be exerted on colored corn when pollinated from races with colorless endosperm, because of certain experiments on variegated xenia which will be described presently.

These experiments of De Vries, Correns, Webber, and others have established experimentally the facts of xenia and Nawaschin's theory of double fertilization seems to offer the only explanation of the phenomenon. But it was left to Guignard (:01) to make the concluding observation that a second sperm nucleus does actually enter into the composition of the endosperm of maize, and this fact clinched the argument which up to this time had been a speculation.

Webber has made a very important addition to the theory of "double fertilization" as an explanation of xenia in some observations and speculations on a mottled condition which is sometimes present when white corns are pollinated by colored. He found that the color was sometimes only transmitted in spots as when Hickory King was pollinated by Cuzco, or perhaps only half a kernel may be colored. Webber offers the hypothesis that the second sperm nucleus may enter the embryo-sac but instead of uniting with the two polar nuclei to form a triple fusion may itself divide separately and thus gives rise to a progeny very different from the other endosperm nuclei. There might then be two sets of nuclei in the endosperm one of which is composed of nuclei which would come directly from the male parent. These latter then might become distributed throughout the embryo-sac but would tend to remain in groups as multiplication progressed and would certainly be expected to influence the character of the tissue which is formed later when the walls are developed around the free nuclei. As Webber expresses it, there might be formed islands of tissue in the endosperm whose cells contain nuclei derived directly from the second sperm and such tissue would be expected to show characters of the male parent in spots as xenia. Again, if the sperm nucleus should unite with only one of the polar nuclei and the other should give rise to an independent progeny we should expect similar mixed conditions in the endosperm, with xenia only expressed in the areas dominated by nuclei containing material derived from the sperm.

There have been reported illustrations of xenia in tissues outside of the endosperm but we are fully justified in awaiting their confirmation before accepting them, especially since some

have failed to stand the test of critical investigation, in the light of the present theory. Thus certain investigators have reported xenia in the color of the seed coats of certain peas. But Giltay ('93) in a series of experiments found no instance where color was transmitted to these tissues. The pigments in these plants lie in the cotyledons of the embryo which of course are readily visible through the thin coats of the seed. While the present theory of xenia is very recent and has been critically applied in few forms, it seems thoroughly satisfactory in every particular with no clearly established evidence against it.

LITERATURE CITED IN SECTION V, "THE PLANT CELL."

ALLEN.
:**04**. Chromosome Reduction in *Lilium canadense*. *Bot. Gaz.*, vol. 37, p. 464.

ALLEN.
:**05**. Nuclear Division in the Pollen Mother-Cells of *Lilium canadense*. *Annals of Bot.*, vol. 19, p. 189.

ATKINSON.
'99. Studies on Reduction in Plants. *Bot. Gaz.*, vol. 29, p. 1.

BAUMGARTNER.
:**04**. Some New Evidence for the Individuality of the Chromosomes. *Biol. Bull.*, vol. 8, p. 1.

BELAJEFF.
'98. Ueber die Reductionstheilung des Pflanzenkernes. *Ber. d. deut. bot. Gesellsch.*, vol. 16, p. 27.

BEARD.
'95. On the Phenomena of Reproduction in Animals and Plants. Antithetic Alternation of Generations. *Annals of Bot.*, vol. 9, p. 441.

BERGHS.
:**04a**. Depuis le spirem jusqu'aux chromosomes mûrs dans la microsporogénèse d'*Allium fistulosum* et de *Lilium lancifolium* (*speciosum*). *La Cellule*, vol. 21, p. 173.

BERGHS.
:**04b**. Depuis la sporogonie jusqu'au spireme définitif dans la microsporogénèse de l'*Allium fistulosum*. *La Cellule*, vol. 21, p. 383.

BERGHS.
:05. La microsporogénèse de *Convallaria maialis*. *La Cellule*, vol. 22, p. 43.

BITTER.
:04. Parthenogenesis und Variabilität der *Bryonia dioica*. Abh. nat. Ver. Brem., vol. 18, p. 99.

BLACKMAN.
:04a. On the Fertilization, Alternation of Generations, and General Cytology of the Uredineæ. *Annals of Bot.*, vol. 18, p. 323.

BLACKMAN.
:04b. On the Relation of Fertilization to "Apogamy" and "Parthenogenesis." *New Phytologist*, vol. 3, p. 149.

BOVERI.
:02. Ueber mehrpolige Mitosen als Mittel zur Analyse des Zellkerns. *Verh. d. phys.-med. Gesellsch. Würzburg.*, vol. 35.

BOVERI.
:04. Ergebnisse über die Konstitution der chromatischen Substanz des Zellkerns. Jena, 1904.

BOWER.
'86. On Apospory in Ferns. *Jour. Linn. Soc. London, Bot.*, vol. 21, p. 360.

BOWER.
'87. On Apospory and Allied Phenomena. *Trans. Linn. Soc. London, Bot.*, II, vol. 2, p. 301.

BOWER.
'88. On some Normal and Abnormal Developments of the Oöphyte in Trichomanes. *Annals of Bot.*, vol. 1, p. 269.

BRIZI.
'92. Apunti di teratologia briologica. *Ann. d. Instit. Bot. d. Roma*, vol. 5, p. 53.

CALKINS.
'97. Chromatin Reduction and Tetrad-formation in Pteridophytes. *Bull. Torrey Bot. Club*, vol. 24, p. 101.

CALKINS.
:01. The Protozoa. New York, 1901.

CHAMBERLAIN.
:05. Alternation of Generations in Animals from a Botanical Standpoint. *Bot. Gaz.*, vol. 39, p. 137.

CANNON.
:02. A Cytological Basis for the Mendelian Laws. *Bull. Torrey Bot. Club*, vol. 29, p. 657.

CANNON.
:03a. The Spermatogenesis of Hybrid Cotton. *Bull. Torrey Bot. Club*, vol. 30, p. 133.

CANNON.
:**03b**. The Spermatogenesis of Hybrid Peas. *Bull. Torrey Bot. Club*, vol. 30, p. 519.
CORRENS.
'99a. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stechlinge. Jena, 1899.
CORRENS.
'99b. Untersuchungen über die Xenien bei *Zea Mays*. *Ber. d. deut. bot. Gesellsch.*, vol. 17, p. 410.
CORRENS.
:**01**. Bastarde zwischen Maisrassen mit besonderer Berücksichtigung der Xenia. *Bibliotheca botanica*, Heft 53. Stuttgart, 1901.
COULTER AND CHAMBERLAIN.
:**03**. Morphology of the Angiosperms. New York, 1903.
COULTER AND LAND.
:**05**. Gametophytes and Embryo of *Torreya taxifolia*. *Bot. Gaz.*, vol. 39, p. 161.
DAVIS.
'96. Development of the Procarp and Cystocarp in the genus Ptilota. *Bot. Gaz.*, vol. 22, p. 353.
DAVIS.
'99. The Spore Mother-Cell of Anthoceros. *Bot. Gaz.*, vol. 28, p. 89.
DAVIS.
:**01a**. Nuclear Studies on Pellia. *Annals of Bot.*, vol. 15, p. 147.
DAVIS.
:**01b**. The Origin of Sex in Plants. *Pop. Sci. Month.*, vol. 60, p. 66.
DAVIS.
:**03a**. The Evolution of Sex in Plants. *Pop. Sci. Month.*, vol. 62, p. 300.
DAVIS.
:**04a**. Oögenesis in Vaucheria. *Bot. Gaz.*, vol. 38, p. 81.
DE BARY.
'78. Ueber apogame Farne und die Erscheinung der Apogamie in Allgemeinen. *Bot. Zeit.*, vol. 36, p. 449.
DE VRIES.
'99. Sur la fécondation hybride de l'albumen. *Compt. Rend. d. Sean. d. l'Acad. d. Sci.*, vol. 129, p. 973.
DE VRIES.
:**00**. Sur la fécondation hybride de l'endosperm chez le maïs. *Rev. Gen. d. Bot.*, vol. 12, p. 129.
DE VRIES.
:**03**. Befruchtung und Bastardierung. Leipzig, 1903.
DIXON.
'95. The Nuclei of *Lilium longiflorum*. *Annals of Bot.*, vol. 9, p. 663.

DIXON.
'96. On the Chromosomes of *Lilium longiflorum*. *Proc. Roy. Irish Acad.*, vol. 3, p. 707.

DIXON.
:00. On the First Mitosis of the Spore Mother-cells of Lilium. *Proc. Roy. Irish Acad.*, vol. 6, p. 1.

DRUERY.
'86a. Observations on a Singular Mode of Development in the Lady-fern (*Athyrium filix-fœmina*). *Jour. Linn. Soc. London, Bot.*, vol. 21, p. 354.

DRUERY.
'86b. Further Notes on a Singular Mode of Reproduction in *Athyrium filix-fœmina*, var. *clarissima*. *Jour. Linn. Soc. London, Bot.*, vol. 21, p. 358.

DRUERY.
'93 Notes on an Aposporous Lastrea (Nephrodium). *Jour. Linn. Soc. London, Bot.*, vol. 29, p. 479.

DRUERY.
'95. Notes upon Apospory in a Form of *Scolopendrium vulgare*, var. *crispum*, etc. *Jour. Linn. Soc. London, Bot.*, vol. 30, p. 281.

DRUERY.
:01. Fern Variation in Great Britain. *Bot. Gaz.*, vol. 31, p. 347.

ERNST.
:01. Beiträge zur Kenntniss der Entwickelung des Embryosackes und des Embryo (Polyembryonie) von *Tulipa gesneriana* L. *Flora*, vol. 88, p. 37.

FARLOW.
'74. An Asexual Growth from the Prothallus of *Pteris cretica*. *Quart. Jour. Mic. Sci.*, vol. 14, p. 266.

FARLOW.
'89. Apospory in *Pteris aquilina*. *Annals of Bot.*, vol. 2, p. 383.

FARMER.
'94. Studies in Hepaticæ: On *Pallavicinia decipiens* Mitten. *Annals of Bot.*, vol. 8, p. 35.

FARMER.
'95a. Spore-formation and Karyokinesis in Hepaticæ. *Annals of Bot.*, vol. 9, p. 363.

FARMER.
'95b. On Spore-formation and Nuclear Division in the Hepaticæ. *Annals of Bot.*, vol. 9, p. 469.

FARMER.
'95c. Further Investigations on Spore-formation in *Fegatella conica*. *Annals of Bot.*, vol. 9, p. 666.

FARMER.
'95d. Ueber Kerntheilung in Lilium-antheren, besonders in Bezug auf die Centrosomenfrage. *Flora*, vol. 80, p. 56.

FARMER AND MOORE.

'95. On the Essential Similarities existing between the Heterotype Divisions in Animals and Plants. *Anat. Anzeig.*, vol. 11, p. 71.

FARMER AND MOORE.

:03. New Investigations into the Reduction Phenomena of Animals and Plants. *Proc. Roy. Soc. London*, vol. 72, p. 104.

FARMER AND MOORE.

:05. On the Maiotic Phase (Reduction Division) in Animals and Plants. *Quart. Jour. Mic. Sci.*, vol. 48, p. 489.

FARMER, MOORE, AND DIGBY.

:03. On the Cytology of Apogamy and Apospory. *Proc. Roy. Soc. London*, vol. 71, p. 453.

FARMER AND WILLIAMS.

'98. Contributions to our Knowledge of the Fucaceæ: their Life-history and Cytology. *Phil. Trans. Roy. Soc. London*, vol. 190, p. 623

FERGUSON.

:04. Contributions to the Knowledge of the Life History of Pinus with Special Reference to Sporogenesis, the Development of the Gametophytes and Fertilization. *Proc. Washington Acad. Sci.*, vol. 6, p. 1.

GILTAY.

'93. Ueber den directen Einfluss des Pollen auf Frucht und Samenbildung. *Jahrb. f. wiss. Bot.*, vol. 25, p. 489.

GRÉGOIRE.

'99. Les cinèses polliniques chez les Liliacées. *La Cellule*, vol. 16, p. 235.

GRÉGOIRE.

:04. La reduction numérique des chromosomes et les cinèses de maturation. *La Cellule*, vol. 21, p. 297.

GREGORY.

:04. Spore Formation in Leptosporangiate Ferns. *Annals of Bot.*, vol. 18, p. 445.

GUIGNARD.

'84. Recherches sur la structure et la division du noyau cellulaire. *Ann. d. Sci. Nat., Bot.*, ser. 6, vol. 17, p. 5.

GUIGNARD.

'85. Nouvelles recherches sur le noyau cellulaire, etc. *Ann. d. Sci. Nat., Bot.*, ser. 6, vol. 20, p. 310.

GUIGNARD.

'89. Étude sur les phenomènes morphologique de la fécondation. *Bull. Soc. Bot. d. France*, vol. 36, p. 106.

GUIGNARD.

'91. Nouvelles études sur la fécondation. *Ann. d. Sci. Nat., Bot.*, ser. 7, vol. 14, p. 163.

GUIGNARD.
'99a. Le développement du pollen et la réduction chromatique dans le *Naias major*. *Arch. d'Anat. Mic.*, vol. 2, p. 455.

GUIGNARD.
'99b. Sur les anthérozoïdes et la double copulation sexuelle chez les végétaux angiospermes. *Compt. Rend.*, vol. 128, p. 864.

GUIGNARD.
:01. La double fécondation dans le maïs. *Jour. Bot.*, vol. 15, p. 37.

HAECKER.
'98. Ueber vorbreitende Theilungsvorgänge bei Thieren und Pflanzen. *Verh. d. deut. zool. Gesellsch.*, vol. 8, p. 94.

HEGELMAIER.
'97. Zur Kenntniss der Polyembryonie von *Allium odorum*, L. *Bot. Zeit.*, vol. 55, p. 133.

ISHIKAWA.
'97. Die Entwickelung der Pollenkörner von *Allium fistulosum*, L., ein Beitrag zur Chromosomenreduktion im Pflanzenreiche. *Jour. Coll. Sci. Imp. Univ. Tokyo*, vol. 10, p. 193.

JUEL.
'98. Parthenogenesis bei *Antennaria alpina* (L.) R. Br. *Bot. Centralb.*, vol. 74, p. 369.

JUEL.
:00. Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung Antennaria. *Handl. Sven Vetensk. Akad.*, vol. 33.

JUEL.
:04. Die Tetradentheilung in der Samenanlage von Taraxacum. *Ark. f. Bot. K. Svenska Vetens. Akad.*, vol. 2, no. 4.

KOENICKE.
:04. Die neueren Arbeiten über die Chromosomenreduction im Pflanzenreich und daran anschliessende karyokinetische Probleme. *Bot. Zeit.*, vol. 62, p. 305.

LANG.
'98. On Apogamy and the Development of Sporangia upon Fern Prothalli. *Phil. Trans. Roy. Soc. London*, ser. B, vol. 190, p. 187.

LANG.
:01. On Apospory in *Anthoceros lævis*. *Annals of Bot.*, vol. 15, p. 503.

LLOYD.
:02. The Comparative Embryology of the Rubiaceæ. *Mem. Torrey Bot. Club*, vol. 8, p. 27.

LOTSY.
'99. *Belanophora globosa* Jungh. Eine wenigsten örtlich-verwittwete Pflanze. *Ann. Jar. Bot. Buiten.*, ser. 2, vol. 1, p. 174.

LOTSY.
: **03**. Parthenogenesis bei *Gnetum ula* Brogn. *Flora*, vol. 92, p. 397.
LOTSY.
: **04**. Die Wendung der Dyaden beim Reifung der Tiereier als Stütze für die Bivalenz der Chromosomen nach der numerischen Reduktion. *Flora*, vol. 93, p. 65.
LOTSY.
: **05**. Die x-Generation und die 2x-Generation. Eine Arbeitshypothese. *Biol. Centralb.*, vol. 25, p. 97.
LYON.
: **04**. The Evolution of Sex Organs in Plants. *Bot. Gaz.*, vol. 37, p. 280.
MCCLUNG.
: **02**. The Accessory Chromosome — Sex Determinant? *Biol. Bull.*, vol. 3, p. 43.
MCCLURE.
'92. Corn Crossing. *Ill. Agric. Exp. Sta. Bull.* 21.
MOENKHAUS.
: **04**. The Development of the Hybrids between *Fundulus heteroclitus* and *Menidia notata* with Especial Reference to the Behavior of the Maternal and Paternal Chromosomes. *Amer. Jour. Anat.*, vol. 3, p. 29.
MONTGOMERY.
: **01**. A Study of the Chromosomes of the Germ Cells of Metazoa. *Trans. Amer. Phil. Soc.*, vol. 20, p. 154.
MONTGOMERY.
: **04**. Some Observations and Considerations upon the Maturation Phenomena of the Germ Cells. *Biol. Bull.*, vol. 6, p. 137.
MOORE, A. C.
: **03**. The Mitoses in the Spore Mother-cell of Pallavicinia. *Bot. Gaz.*, vol. 36, p. 384.
MOTTIER.
'97. Beiträge zur Kenntniss der Kerntheilung in den Pollenmutterzellen einiger Dikotylen und Monokotylen. *Jahrb. f. wiss. Bot.*, vol. 30, p. 169.
MOTTIER.
: **03**. The Behavior of the Chromosomes in the Spore Mother-cells of Higher Plants and the Homology of the Pollen and Embryo-sac. Mother-cells. *Bot. Gaz.*, vol. 35, p. 250.
MURBECK.
: **01a**. Parthenogenetische Embryobildung in der Gattung Alchemilla. *Lunds. Univ. Arsskrift*, vol. 36.
MURBECK.
: **01b**. Ueber das Verhalten des Pollenschlauches bei *Alchemilla arvensis* (L.) Scop. und das Wesen der Chalozogamie. *Lunds. Univ Arsskrift*, vol. 36.

MURBECK.
:02. Ueber Anomalien im Baue des Nucellus und des Embryosackes bei parthenogenetischen Arten der Gattung Alchemilla. *Lunds. Univ. Arsskrift*, vol. 38.

MURBECK.
:04. Parthenogenese bei den Gattungen Taraxacum und Hieracium. *Botan. Not.*, 1904, p. 285.

NATHANSOHN.
:00. Ueber Parthenogenesis bei Marsilia und ihre Abhängigkeit von der Temperatur. *Ber. d. deut. bot. Gesellsch.*, vol. 18, p. 99.

NAWASCHIN.
'98. Resultate einer Revision der Befruchtungsvorgänge bei *Lilium martagon* und *Fritillaria tenella*. *Bull. Acad. Imp. Sci. St. Petersb.*, vol. 9, p. 377.

OSTENFELD.
:04a. Zur Kenntniss der Apogamie in der Gattung Hieracium. *Ber. d. deut. bot. Gesellsch.*, vol. 22, p. 376.

OSTENFELD.
:04b. Weitere Beiträge zur Kenntniss der Fruchtentwicklung bei der Gattung Hieracium. *Ber. d. deut. bot. Gesellsch.*, vol. 22, p. 537.

OVERTON, E.
'93a. Ueber die Reduction der Chromosomen in den Kernen der Pflanzen. *Vierteljahrssch. d. naturf. Gesellsch. Zurich*, vol. 38.

OVERTON, E.
'93b. On the Reduction of the Chromosomes in the Nuclei of Plants. *Annals of Bot.*, vol. 7, p. 139.

OVERTON, J. B.
:02. Parthenogenesis in *Thalictrum purpurascens*. *Bot. Gaz.*, vol. 33, p. 363.

OVERTON, J. B.
:04. Ueber Parthenogenesis bei *Thalictrum purpurascens*. *Ber. d. deut. bot. Gesellsch.*, vol. 22, p. 274.

PRINGSHEIM.
'76. Ueber vegetative Sprossung der Moosfrüchte. *Monatsber. d. k. Akad. d. Wiss. Berlin*, 1876, p. 425.

RAUNKIAER.
:03. Kimdannelse uden Befrugtning hos Mælkebötte (Taraxacum). *Bot. Tidsskr.*, vol. 25, p. 109.

ROBERTSON.
:04. Studies on the Morphology of *Torreya californica* Torrey. II. The Sexual Organs and Fertilization. *New Phytologist*, vol. 3, p. 205.

ROSENBERG.
:03a. Das Verhalten der Chromosomen in einer hybriden Pflanze. *Ber. d. deut. bot. Gesellsch.*, vol. 21, p. 110.

ROSENBERG.

:**03b**. Ueber die Befruchtung von *Plasmopara alpina* (Johans.). *Bihang til K. Svenska Vet.-Akad. Hand.*, vol. 28, Afd. 3, No. 10.

ROSENBERG.

:**04a**. Ueber die Tetradenteilung eines Drosera-bastardes. *Ber. d. deut. bot. Gesellsch.*, vol. 22, p. 47.

ROSENBERG.

:**04b**. Ueber die Reduktionsteilung in Drosera. *Meddel. Stock. Hogs. Bot. Inst.*, 1904.

ROSENBERG.

:**05**. Zur Kenntniss der Reduktionsteilung in Pflanzen. *Bot. Notis.*, part 1, 1905.

SADEBECK.

'**79**. Schenk's Handbuch der Botanik, Breslau 1897. [An Account of Apogamy in Ferns]. Vol. 1, p. 231.

SARGANT.

'**96**. The Formation of the Sexual Nuclei in *Lilium martagon*. I. Oögenesis. *Annals of Bot.*, vol. 10, p. 445.

SARGANT.

'**97**. The Formation of Sexual Nuclei in *Lilium martagon*. II. Spermatogenesis. *Annals of Bot.*, vol. 11, p. 187.

SCHAFFNER.

'**97**. The Division of the Macrospore Nucleus (of *Lilium philadelphicum*). *Bot. Gaz.*, vol. 23, p. 430.

SCHOENFELD.

:**01**. La spermatogénèse chez le taureau et chez les mammifères en général. *Arch. d. Biol.*, vol. 18, p. 1.

SCHREINER AND SCHREINER.

:**04**. Die Reifungsteilung bei den Wirbeltieren. Ein Beitrag zur Frage nach der Chromatinreduktion. *Anat. Anz.*, vol. 24, p. 561.

SHAW.

'**97**. Parthenogenesis in Marsilia. *Bot. Gaz.*, vol. 24, p. 114.

STAHL.

'**76**. Ueber künstlich hervorgerufene Protonemabildung an dem Sporogonium der Laubmoose. *Bot. Zeit.*, vol. 34, p. 689.

STRASBURGER.

'**84**. Neuere Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen als Grundlage für eine Theorie der Zeugung. Jena, 1884.

STRASBURGER.

'**88**. Ueber Kern- und Zelltheilung in Pflanzenreiche nebst einem Anhang über Befruchtung. *Hist. Beitr.*, Heft 1. Jena, 1888.

STRASBURGER.

'**94a**. The Periodic Reduction of the Number of Chromosomes in the Life-history of Living Organisms. *Annals of Bot.*, vol. 8, p. 281.

STRASBURGER.
'94b. Ueber periodische Reduktion der Chromosomenzahl in Entwicklungsgang der Organismen. *Biol. Centralb.*, vol. 14, pp. 817 and 849.

STRASBURGER.
'95. Karyokinetische Probleme. *Jahrb. f. wiss. Bot.*, vol. 28, p. 151.

STRASBURGER.
'97a. Kerntheilung und Befruchtung bei Fucus. *Jahrb. f. wiss. Bot.*, vol. 30, p. 351.

STRASBURGER.
'97b. Ueber Cytoplasmastrukturen, Kern- und Zelltheilung. *Jahrb. f. wiss. Bot.*, vol. 30, p. 375.

STRASBURGER.
'97c. Ueber Befruchtung. *Jahrb. f. wiss. Bot.*, vol. 30, p. 406.

STRASBURGER.
.00a. Ueber Reduktionstheilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich. *Hist. Beitr.*, Heft 6. Jena, 1900.

STRASBURGER.
:00b. Einige Bemerkungen zur Frage nach der doppelten Befruchtung bei den Angiospermen. *Bot. Zeit.*, vol. 58, p. 293.

STRASBURGER.
:01. Ueber Befruchtung. *Bot. Zeit.*, vol. 59, p. 353.

STRASBURGER.
:04a. Anlage des Embryosackes und Prothalliumbildung bei der Eibe nebst ausschliessenden Erörterungen. *Fest. z. 70th Geburtstag Haeckel.*

STRASBURGER.
:04b. Ueber Reduktionsteilung. *Sitzber. Akad. Berlin*, vol. 18, p. 587.

STRASBURGER.
:04c. Die Apogamie der Eualchemillen und allgemeine Gesichtspunkte die sich aus ihr ergeben. *Jahrb. f. wiss. Bot.*, vol. 41, p. 88.

STRASBURGER AND MOTTIER.
'97. Ueber den zweiten Theilungsschritt in Pollenmutterzellen. *Ber. d. deut. bot. Gesellsch.*, vol. 15, p. 327.

SUTTON.
:02. On the Morphology of the Chromosome Group in *Brachystola magna*. *Biol. Bull.*, vol. 4, p. 24.

SUTTON.
:03. The Chromosomes in Heredity. *Biol. Bull.*, vol. 4, p. 231.

TRETJAKOW.
'95. Die Betheiligung der Antipoden in Fällen der Polyembryonie bei *Allium odorum* L. *Ber. d. deut. bot. Gesellsch.*, vol. 13, p. 13.

TREUB.
'98. L'organe femelle et l'apogamie du *Belanophora elongata* Bl. *Ann. Jard. Bot. Buiten.*, vol. 15, p. 1.

TREUB.

:**02**. L'organe femelle et l'embryogénèse dans le *Ficus hirta* Vahl. *Ann. Jard. Bot. Buiten.*, ser. 2, vol. 3, p. 124.

TROW.

:**04**. On Fertilization in the Saprolegnieæ. *Annals of Bot.*, vol. 18, p. 541.

WEBBER.

:**00**. Xenia, or the Immediate Effect of Pollen in Maize. *U. S. Dept. Agric., Div. Veg. Path. Phys., Bull. 22.*

WILLIAMS.

:**04a**. Studies in the Dictyotaceæ. I. The Cytology of the Tetrasporangium and the Germinating Tetraspore. *Annals of Bot.*, vol. 18, p. 141.

WILLIAMS.

:**04b**. Studies in the Dictyotaceæ. II. The Cytology of the Gametophyte Generation. *Annals of Bot.*, vol. 18, p. 183.

WILSON.

:**00**. The Cell in Development and Inheritance. New York, 1900.

WINIWARTER.

:**00**. Recherches sur l'ovogénèse et l'organogénèse de l'ovaire des mammifères (lapin et homme). *Arch. d. Biol.*, vol. 17, p. 33.

WINKLER.

:**01**. Ueber Merogonie und Befruchtung. *Jahrb. f. wiss. Bot.*, vol. 36, p. 753.

WINKLER.

:**04**. Ueber Parthenogenesis bei *Wikstræmia indica* (L.) C. A. Mey. *Ber. d. deut. bot. Gesellsch.*, vol. 22, p. 573.

WOLFE.

:**04**. Cytological Studies on Nemalion. *Annals of Bot.*, vol. 18, p. 607.

NOTES AND LITERATURE.

NATURE STUDY.

Nature Study.[1]—Two little text books on nature study, designed for use in the lower grammar school grades, give evidence of the progress which has been made during the last decade in laying the foundation for the teaching of the natural sciences. Too often in our public and private schools a teacher is expected to give her pupils "nature work," whether she herself is interested in the subject or trained for it. To such, if they have the gift of teaching, these books should prove helpful. Dr. Overton's in particular cannot fail to be stimulating to both teacher and pupil. It contains a series of thirty-two lessons on various simple phenomena of plant and insect life. Carter's *Nature Study with Common Things* is intended especially for city schools. It contains seventeen lessons on material taken exclusively from plant life, either the fruit or that part of the plant in which nutriment is stored. In the hands of an unskilful teacher this course could easily become a burden to the young pupil, inasmuch as it is limited to a field usually uninteresting to children. The following quotation from Dr. Overton's preface brings out one point frequently overlooked in a discussion of nature study; the italics are our own. "The object of nature study," says Dr. Overton, "is not so much to get present knowledge as to develop the power *and love* of observation by which knowledge may be gained in after life."

R. H.

[1] Overton, Frank. Assisted by Mary E. Hill. *Nature Study. A Pupil's Textbook.* New York, American Book Company, 1905. 142 pp., illus.

Carter, M. H. *Nature Study with Common Things. An Elementary Laboratory Manual.* New York, American Book Company, 1904. 150 pp., illus.

ZOÖLOGY.

Wasps Social and Solitary.[1] — Rarely has such a fascinating book as this on a given subject of natural history been presented to the lovers of nature studies. So clearly and charmingly written, it is a work from which all can derive pleasure and instruction. The amount of time and patience required to obtain a knowledge of the life habits of the various species can only be appreciated by one who has attempted to work out a few species bearing indirectly on another order of insects.

The varied habits of the wasps, from earth-diggers to wood-borers, and from masons to paper-makers, give one every opportunity of coming in contact with some of them during the many summer rambles, and often to observe them under the most favorable circumstances. Their methods of paralyzing other insects and spiders which they transport to their nests as food for their larvæ, suggests both surgical and engineering skill; equally interesting is the fact that each species selects certain kinds of food for its progeny; one captures spiders only, another the larvæ of Lepidoptera, a third flies, and others beetles or bugs. "So strong and deeply seated is the preference that no fly-robber ever takes spiders, nor will the ravisher of the spiders change to beetles or bugs."

The activities of the wasp are arranged under two groups:— "Instincts and Acts of Intelligence, it being understood that these classes pass by insensible stages into each other." Under the first are included stinging, the particular methods of attacking and paralyzing the prey, selecting the proper food, mode of carrying booty, the general style of nest, spinning of cocoons, etc. To distinguish acts of intelligence requires a familiarity with the normal conditions of the insect. Such modifications of instinct as the adaptation of the mud-daubers (Pelopæus) to the rafters and chimneys of buildings, the Trypoxylon taking advantage of the straws on the face of a stack that had been cut off smoothly, the hanging of spiders in a plant to avoid the attacks of ants while searching for a nesting-place, the occasional occupation by a queen Polistes of the previous year's comb instead of building a new one, the almost universal habit of Bembex of closing the openings to their burrows when leaving, and

[1] Peckham, George W., and Elizabeth G. *Wasps Social and Solitary.* With an introduction by John Burroughs. Boston and New York, Houghton, Mifflin & Co., 1905. 12mo, xv + 311 pp., illus.

of Pompilus of enlarging its nest to accommodate an unusually large spider, and of Ammophiles in seizing a small pebble in its mandible and pounding down the earth over the opening to its nest, would all come under the second group.

In summing up the chapter on the instinct and intelligence of wasps, the authors who have so entertainingly presented the facts, leave it largely to the reader "to determine whether the wasps are wiser than they seem or seem wiser than they are."

C. W. J.

Trouessarts' Catalogus Mammalium, Supplement.[1] — The great activity of the last few years in discovering and describing new species of mammals, living and fossil, has necessitated the preparation of a "quinquennial supplement" to include changes and additions made since the publication of the 1897 catalogue. The first three fascicles of this supplement list the known living and fossil Primates, Prosimiæ, Chiroptera, Insectivora, Carnivora (Fasc. 1); the Rodentia (Fasc. 2); the Tillodontia, Ungulata, and Sirenia (Fasc. 3). The fourth fascicle will conclude the work and will contain an index. In the preface the author states that the present supplement is intended to summarize the state of our knowledge on this subject to date of January 1, 1903, though in fascicle 3 certain new genera and species described in 1904, are included without explanation, *e. g.*, Nesohippus Amegh. (p. 635). In addition to listing the new forms, all the species noted in the edition of 1897–99 are given in their proper place, each with its serial number, but instead of the list of references following, there is added simply a number referring to the full quotations for the species given in the former list, in cases where no change has been made. A new feature introduced in the present supplement is the citation of the full reference in case of generic and subgeneric names. Footnotes and explanatory remarks are in French, not in Latin as in the previous edition.

In general the compiler has made no attempt at revisionary work so far as concerns specific determinations, but some care has been used in replacing unavailable generic and subgeneric names with new or later ones. Thus, in including Matschie's revision of the anthropoid apes, Trouessart does not repeat that author's error of

[1] Trouessart, E. L. *Catalogus Mammalium tam Viventium quam Fossilium. Quinquennale Supplementum, Anno 1904.* Berlin, R. Friedländer & Sohn, 1904–1905. Fasc. 1–3, 8vo, iv + 752 pp. 12 Mk. per fasc.

adopting Troglodytes as the generic name of the chimpanzee, but unfortunately he overlooks the earliest available name, Pan, recently revived by Palmer. Also, the authority for the specific name of *Gorilla gorilla* should be Savage, not Wyman. Midas should not have been used as a name for a mammalian genus, as it is preoccupied among the Lepidoptera. The following new subgeneric names are proposed for Primates: Pogonocebus to replace Diadema, Leptocebus for Semnocebus, Maimon for Mormon, Promioclænus for Mioclænus. Palmer has recently shown, however, that Mandril of Voigt (1831) is available for Mormon, while the same author in 1903 proposed the subgeneric term Lophocebus to replace subgenus Semnocebus.

In the determination of subfamilies, genera, and subgenera, Trouessart frequently follows his own preference, and not always, it would seem, to best advantage. Thus Pipistrellus and Lasionycteris are regarded as subgenera of Vespertilio, and Dasypterus is placed as a subgenus of Lasiurus, while two such closely allied forms as Nycticeius and Rhogeëssa are nevertheless accorded their generic rank. Artibeus is made to include Uroderma and Dermanura as subgenera. Other instances might be multiplied.

Additional new generic and subgeneric names proposed are: Jentinkia to replace Wagneria, Aymardia for Cynodon, Pagophoca for subgenus Pagophilus, Orthægocerus a new subgenus of Capra. The new family name Cœndidæ is proposed instead of Erithizontidæ for the New World porcupines.

Trouessart has made a laudable attempt to sort out so far as may be the numerous new species of Muridæ described in 1900 from Chile by Philippi, mostly under the generic name Mus. One of these names, "*Mus nemoralis*," thought by Trouessart to be an Oxymycterus, is preoccupied by *Mus nemoralis* Blyth, though this seems to have escaped the notice of the compiler. Philippi's "*Cervus brachyceros*" is similarly preoccupied and is renamed by Trouessart, *Odocoileus philippii*.

The questionable practice of amending names leads the compiler to change Tayassu to Tayassus since, he states, barbaric names should be latinized. Nevertheless he rejects Dugong in favor of the retal Halicore on the ground that the former is a barbaric name. It is a pity, however, that it is not possible to exclude such abnormalities as Guilielmofloweria or Carolozittelidæ!

Apparently Miller and Rehn's list of North American land mammals published in 1901 (*Proc. Boston Soc. Nat. Hist.*, vol. 30) was

unknown to the compiler. Comparison with this might have been of considerable value and would have prevented, for example, the omission of *Fiber osoyoosensis* Lord, 1863.

Considering the editorial difficulties presented by a work of this nature, typographical errors are few. Several cases occur, however, in which the prefix denoting fossil species only is inadvertently applied in connection with living forms, *e. g.*, *Lama vicugna* and *Trichechus manatus*. The specific name of the capybara is misspelled four times on p. 529.

The Catalogus gives evidence of laborious and painstaking work throughout, and is indispensable to all working mammalogists. For this reason, however, it is to be regretted that the price (12 Marks per fascicle) is such as to place it beyond the means of many who need it.

G. M. A.

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